Nota Lepi. **41**(1) 2018: 145–179 | DOI 10.3897/nl.41.23090

Agrotis fatidica (Hübner, 1824) species-group revisited, with description of two new species from the Alps and the Pyrenees (Lepidoptera, Noctuidae)

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http://zoobank.org/750FE3C3-5EE2-4E0A-9F27-8A67BA68B5ED

Received 20 December 2017; accepted 19 March 2018; published: 27 June 2018
Subject Editor: Alberto Zilli.

Abstract. An integrative taxonomic analysis of the European species of the *Agrotis fatidica* species-group is presented with special reference to the European sister taxa of *A. fatidica* (Hübner, 1824); in addition, a general overview of the entire species-group is given. The remarkable differences found in the barcodes of the Central and Western European populations of *A. fatidica* (sensu lato) led us to recognise isolated species of the *A. fatidica* complex. Two new species, *A. mayrorum* **sp. n.** (Northern Italy and the French Alps) and *A. mazeli* **sp. n.** (French Pyrenees) are described. The neotype of *A. fatidica* is designated. *Agrotis luehri* von Mentzer & Moberg, 1987 is treated as a subspecies of *A. fatidica* (**stat. n.**).

Introduction

Species identification and delimitation is one of the major issues in taxonomic work. In mega-diverse groups such as Lepidoptera the taxonomic treatment was almost exclusively based on morphology for nearly 250 years, with integrative approaches being rare. Recently developed molecular methods, particularly DNA-barcoding, have changed this tradition dramatically (Hebert et al. 2003, 2009). Identification of species nowadays increasingly considers molecular data, which have proved an excellent method for delimitation of large numbers of Lepidoptera on different continents (e.g. Hausmann et al. 2011a, 2011b; Hebert et al. 2013; Huemer et al. 2014b; Zahiri et al. 2014). The formation of an increasingly complete DNA barcode-library is providing a basic tool to detect cryptic diversity (Huemer 2011; Mutanen et al. 2012, 2013; Huemer and Hebert 2016) and will be a pre-requisite for future taxonomic work.

In the year 2011 the Tiroler Landesmuseum in cooperation with The International Barcode of Life (iBOL) started a campaign to sequence the Lepidoptera fauna of the entire alpine arc. To date, more than 20,000 DNA barcodes of >3500 species have been made available. Over recent years, several overlooked cryptic species have been detected (e.g. Huemer and Hausmann 2009; Huemer and Hebert 2011; Huemer et al. 2013; Huemer et al. 2014a, 2014c; Huemer and Timossi 2014; Buchner 2015; Huemer and Mutanen 2015; Kirichenko et al. 2015; Baldizzone and Landry 2016; Gilligan et al. 2016; Kozlov et al. 2016). In this paper we reveal a striking cryptic diversity in the taxonomically difficult genus *Agrotis* Ochsenheimer, 1816.

Material and methods

Morphology and material

Extensive generic descriptions and diagnoses of Holarctic species of the *Agrotis fatidica* (Hübner, 1824) species-group have been published in several reviews (von Mentzer and Moberg 1987; Fibiger 1990, 1997; Nupponen et al. 2001; Fibiger et al. 2010), and are not repeated here.

Our study is based on about 1,500 specimens of the *Agrotis fatidica* species-group. Most of the material was traditionally set and dried, although a few specimens are pinned but remained unset. Genitalia preparations followed standard techniques for Noctuoidea, including everting the vesica.

DNA sequencing and analysis

Full-length lepidopteran DNA barcode sequences are a 658 base-pair (bp) long segment of the 5' terminus of the mitochondrial COI gene (*cytochrome c oxidase 1*). DNA extracts were prepared from a dried leg of each of 22 specimens of the *Agrotis fatidica* species-group from Europe (12 *A. fatidica*, 2 *A. proverai* Zilli, Fibiger, Ronkay & Yela, 2010, 5 *A. mayrorum* sp. n., 3 *A. mazeli* sp. n., see Table 1.) and processed at the Canadian Centre for DNA Barcoding (CCDB, Biodiversity Institute of Ontario, University of Guelph) to obtain DNA barcodes, using the standard high-throughput protocol described in deWaard et al. (2008). We also used 3 sequences of *Agrotis luehri*

Table 1. List of successfully sequenced material of the *Agrotis fatidica* species-group.

Species	Country	Sample ID	Process ID	BIN	Coll.
Agrotis fatidica	Russia	TLMF Lep 20525	LEALT302-16	BOLD:AAA1629	TLMF
Agrotis fatidica	Russia	TLMF Lep 20524	LEALT301-16	BOLD:AAA1629	TLMF
Agrotis fatidica	Russia	TLMF Lep 20523	LEALT300-16	BOLD:AAA1629	TLMF
Agrotis fatidica	Austria	KLM Lep 03485	ABOLB825-15	BOLD:AAA1629	LMK
Agrotis fatidica	Austria	TLMF Lep 00185	PHLAA145-09	BOLD:AAA1629	TLMF
Agrotis fatidica	Switzerland	TLMF Lep 02702	PHLAC667-10	BOLD:AAA1629	TLMF
Agrotis fatidica	Austria	TLMF Lep 00184	PHLAA144-09	BOLD:AAA1629	TLMF
Agrotis fatidica	Italy	TLMF Lep 00166	PHLAA126-09	BOLD:AAA1629	TLMF
Agrotis fatidica	Austria	TLMF Lep 02972	PHLAC937-10	BOLD:AAA1629	TLMF
Agrotis fatidica	Italy	TLMF Lep 00165	PHLAA125-09	BOLD:AAA1629	TLMF
Agrotis fatidica	Italy	TLMF Lep 15779	LEATH567-14	BOLD:AAA1629	TLMF
Agrotis fatidica	Italy	TLMF Lep 15780	LEATH568-14	BOLD:AAA1629	TLMF
Agrotis fatidica luehri	Norway	NHMO-DAR-9557	LON3613-16	BOLD:AAA1629	NHMO
Agrotis fatidica luehri	Norway	NHMO-DAR-9556	LON3612-16	BOLD:AAA1629	NHMO
Agrotis fatidica luehri	Norway	CNCNoctuoidea13171	RDNMD839-07	BOLD:AAA1629	CNC
Agrotis mayrorum	Italy	TLMF Lep 08820	PHLAI325-13	BOLD:ACE4355	TLMF
Agrotis mayrorum	Italy	TLMF Lep 08647	PHLAH843-12	BOLD:ACE4355	TLMF
Agrotis mayrorum	France	TLMF Lep 16460	PHLAJ405-14	BOLD:ACE4355	TLMF
Agrotis mayrorum	Italy	TLMF Lep 08648	PHLAH844-12	BOLD:ACE4355	TLMF
Agrotis mayrorum	Italy	TLMF Lep 08819	PHLAI324-13	BOLD:ACE4355	TLMF
Agrotis mazeli	France	TLMF Lep 14496	LASTS044-14	BOLD:ACR9899	TLMF
Agrotis mazeli	France	TLMF Lep 14494	LASTS042-14	BOLD:ACR9899	TLMF
Agrotis mazeli	France	TLMF Lep 14495	LASTS043-14	BOLD:ACR9899	TLMF
Agrotis proverai	Italy	TLMF Lep 16459	PHLAJ404-14	BOLD:AAA1629	TLMF
Agrotis proverai	Italy	TLMF Lep 14546	LASTS094-14	BOLD:AAA1629	TLMF

von Mentzer & Moberg, 1987 from BOLD [sample ID´s NHMO-DAR-9557, NHMO-DAR-9557, CNCNoctuoidea1317] for our analysis. All sequences are 658 bp long, except for 4 sequences of *A. fatidica* ranging from 600 bp to 657 bp and one sequence of *A. mazeli* with 581 bp. Sequences were submitted to GenBank; further details including complete voucher data and images can be accessed in the public dataset "Lepidoptera of the Alps - *Agrotis fatidica* species-group" dx.doi.org/10.5883/DS-AGROFATI in the Barcode of Life Data Systems (BOLD; Ratnasingham and Hebert 2007). Degrees of intra- and interspecific variation in the DNA barcode fragment were calculated under Kimura 2 parameter (K2P) model of nucleotide substitution using analytical tools in BOLD systems v3.0. (http://www.boldsystems.org). A neighbour-joining tree of DNA barcode data of selected taxa was constructed using Mega 6 (Tamura et al. 2013).

Photographic documentation

Representative samples of already described European taxa of the *Agrotis fatidica* group and their Asiatic relatives were studied and photographed. Material was examined from several European museums and private collections (see abbreviations below). All specimens dissected during the studies were photographed in colour, as were their genitalia slides. The habitus of the specimens was photographed with a Nikon D90 camera; the images of the genitalia slides were taken with a Nikon Eclipse 80i photomicroscope with a Nikon DS-Fi2 digital camera. All images are preserved in the photographic catalogue of the Heterocera Research Team, Budapest.

Abbreviations of private and institutional collections

BMNH	The Natural History Museum (formerly British Museum, Natural History), London, United Kingdom
CNC	Canadian National Collection of Insects, Arachnids and Nematodes
HNHM	Hungarian Natural History Museum, Budapest, Hungary
LMK	Landesmuseum Kärten, Klagenfurt, Austria
MNHU	Museum für Naturkunde, Humboldt-Universität, Berlin, Germany
NHMO	Natural History Museum, University of Oslo, Norway
NHMW	Naturhistorisches Museum Wien, Austria
RCBS	Research Collection Bjarne Skule, Veksø, Denmark
RCTM	Research Collection Toni Mayr, Feldkirch, Austria
RNS	Royal Natural History Museum (Naturhistoriska Riksmuseet), Stockholm, Sweden
TLMF	Tiroler Landesmuseum Ferdinandeum, Innsbruck, Austria
ZMHU	Museum für Naturkunde – Leibniz-Institut für Evolutions- und Biodiversitätsforschung, Berlin, Germany
ZMUC	Zoological Museum, Natural History Museum of Denmark, Copenhagen, Denmark
ZSM	Zoologische Staatssammlung, Munich, Germany

Checklist of the Palaearctic taxa of the *Agrotis fatidica* species-group

Agrotis fatidica fatidica (Hübner, 1824)
  incurva Herrich-Schäffer, 1851
  monedula Dannehl, 1925
Agrotis fatidica luehri von Mentzer & Moberg, 1987 **stat. n.**
Agrotis proverai Zilli, Fibiger, Ronkay & Yela, 2010
Agrotis mayrorum **sp. n.**
Agrotis mazeli **sp. n.**

Agrotis trifurcula (Staudinger, 1892)
Agrotis innocens (Boursin, 1967)
Agrotis characteristica Alphéraky, 1892
  bombycia Eversmann, 1851
  robusta Eversmann, 1856, nec Blanchard, 1852
  sajana Corti, 1932 (= *sajana* Bang-Haas, manuscript name)
  robustana Poole, 1989
Agrotis iremeli Nupponen, Ahola & Kullberg, 2001
Agrotis ruta (Eversmann, 1851)
  xylographa Boursin, 1947
?*Agrotis patula* (Walker, 1857) (status unclear)
  septentrionalis Möschler, 1862
  kurodakeana (Matsumura, 1927)
  subinformis (Bryk, 1941)

Taxa of the *Agrotis fatidica* (Hübner, 1824) species-group and the history of their interpretation

The taxonomy of the *Agrotis fatidica* (Hübner, 1824) species-group has always been difficult to resolve. There is much similarity in habitus between taxa, slightly polymorphic facies shown by allopatric populations of a putatively identical "species" and remarkable uniformity in genitalia characters between populations. Some of the taxonomic problems concerning the ranking of some populations of the *A. fatidica* species-complex have been partly or satisfactorily solved over the last twenty years (e.g. Fibiger 1997; von Mentzer and Moberg 1987; Nupponen et al. 2001; Kononenko 2005; Fibiger et al. 2010; Lafontaine and Schmidt 2010). The main issues, which remain open and are reviewed here, will be solved probably only after detailed genetic investigations.

The taxa of the *A. fatidica* species-group mentioned in the older and recent literature sources are introduced briefly below, indicating the short history of their interpretation and the basic taxonomic and biogeographical data that led to their relegation.

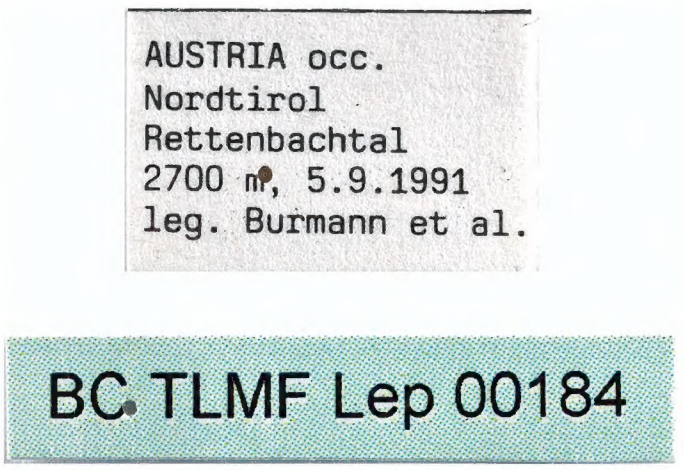
Agrotis fatidica (Hübner, 1824)

Figs 1–8; Gen. figs 1–2, 16

Noctua fatidica was described from an unspecified number of male specimens and figured in colour (Hübner 1824, pl. 152, figs. 704–705). The type-locality is vague ([Europe]) although the traditional concept of *A. fatidica* is based on specimens from the Alps, which is the major source of specimens in collections from the European Continent (see, for instance, Fibiger 1990, 1997; Fibiger et al. 2010).

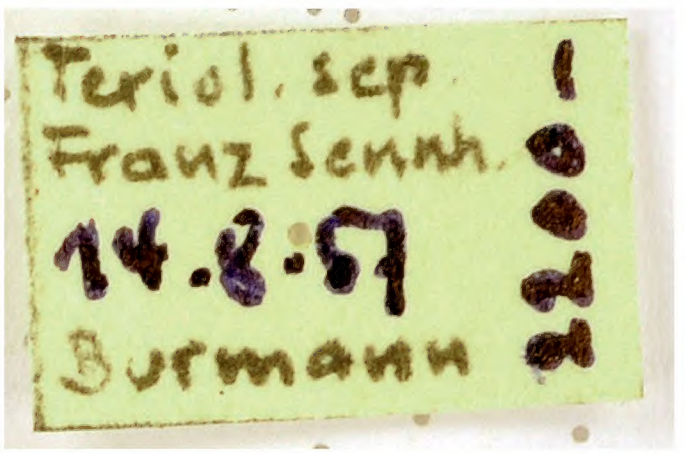
The type material is considered lost (Horn and Kahle 1935–1937) and we here designate a neotype from the eastern Alps in order to maintain stability of the nomenclature and ground the traditional interpretation of "*fatidica*". Such a designation follows the qualifying conditions of section 75.3 of the ICZN Code, 4th edition. We select an Austrian specimen, which is barcoded and which has a sequence that fits well with the DNA barcodes of the other specimens we have investigated. The sequence is in fact identical to those of four specimens.

1. *Agrotis fatidica fatidica* (Hübner, 1824) Neotype male



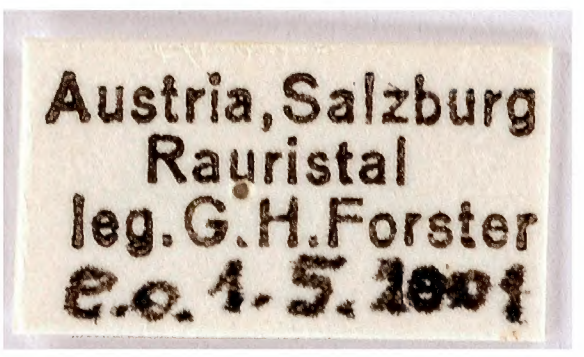
2. *Agrotis fatidica fatidica* (Hübner, 1824) Neotype male, labels

3. *Agrotis fatidica fatidica* (Hübner, 1824) male



4. *Agrotis fatidica fatidica* (Hübner, 1824) male, label

5. *Agrotis fatidica fatidica* (Hübner, 1824) female

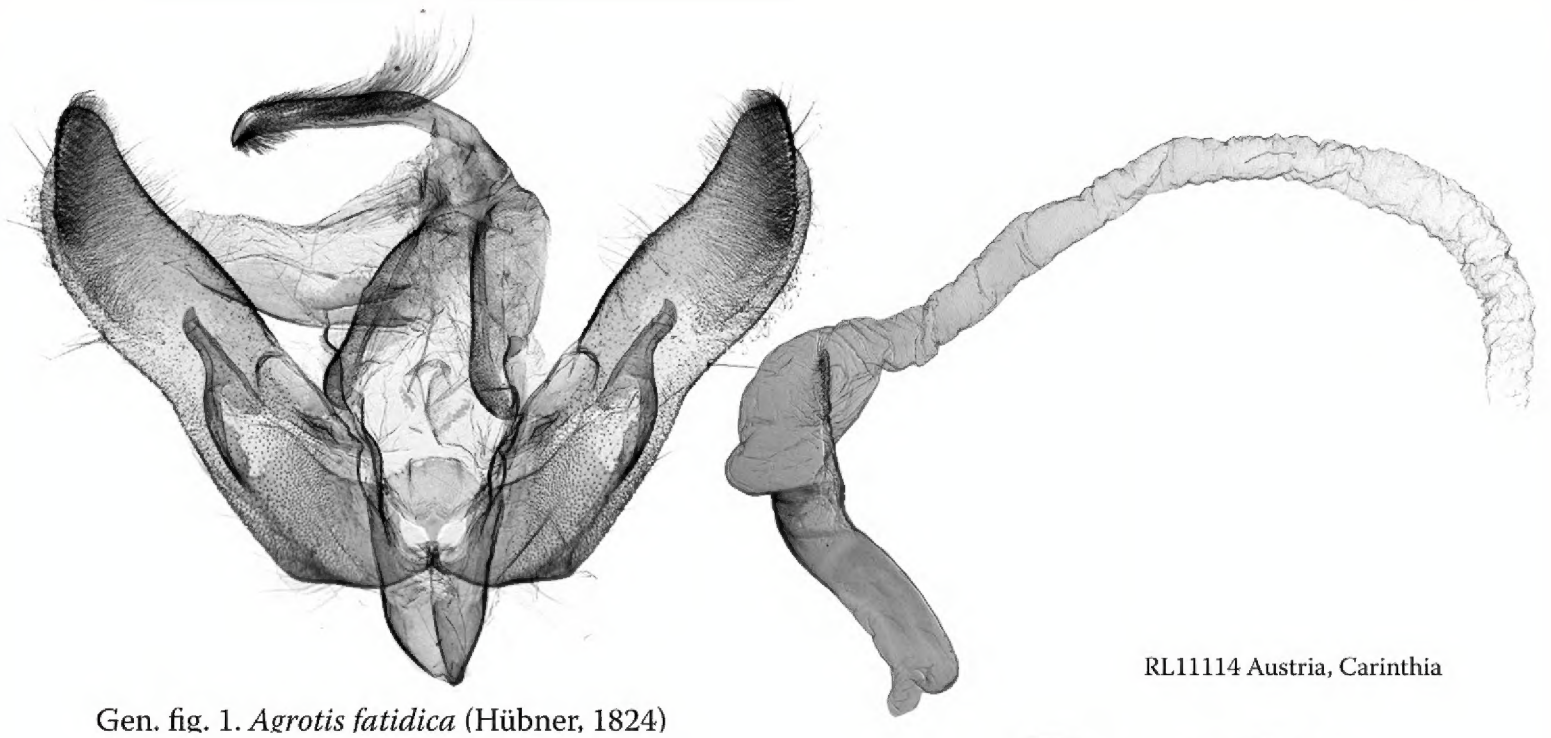


6. *Agrotis fatidica fatidica* (Hübner, 1824) female, label

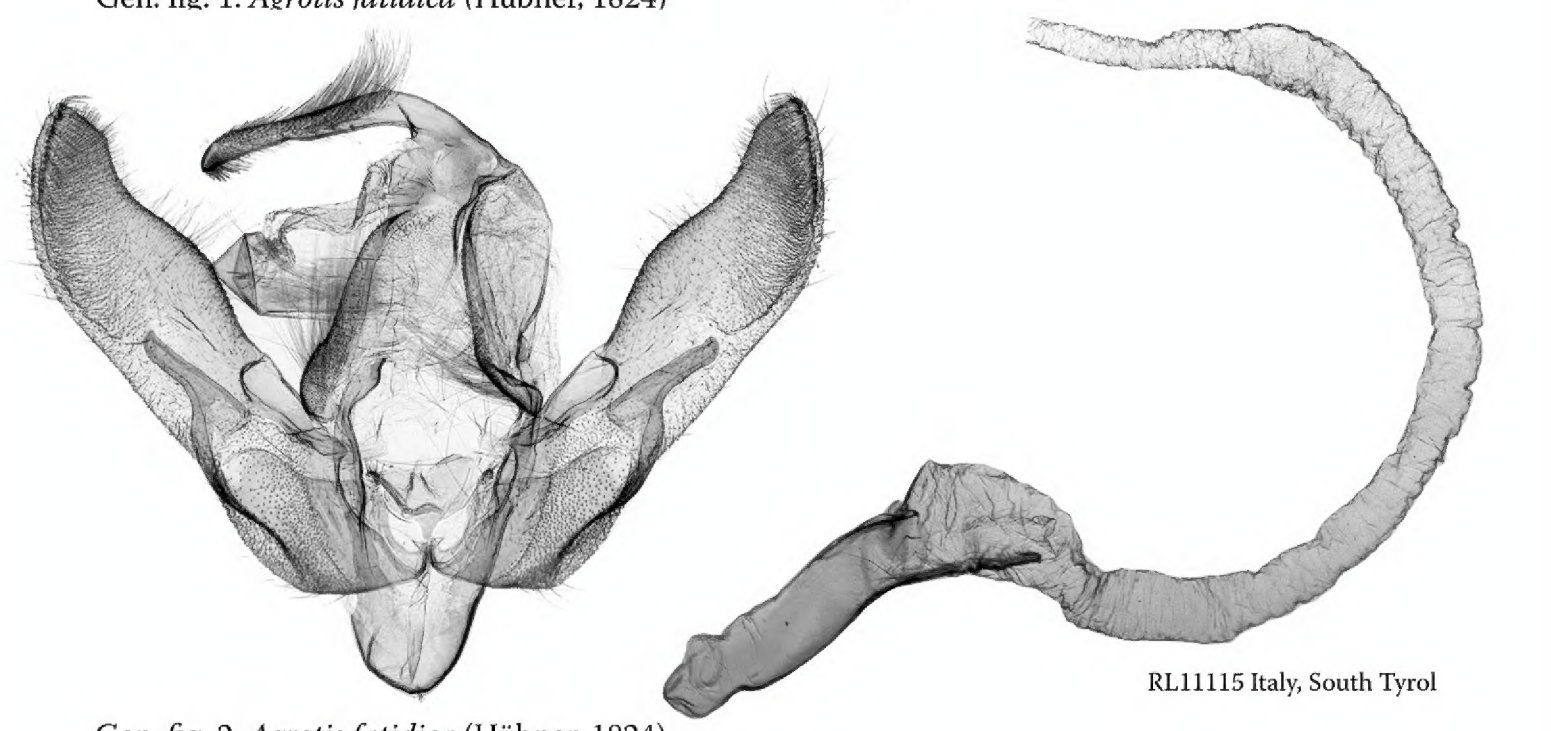
7. *Agrotis fatidica fatidica* (Hübner, 1824) female

8. *Agrotis fatidica fatidica* (Hübner, 1824) female, labels

Figures 1–8. *Agrotis fatidica*. **1–2** Neotype male, Austria, **3–4** male, Austria, **5–6** female, Austria, **7–8** female, Switzerland.



Gen. fig. 1. *Agrotis fatidica* (Hübner, 1824)



Gen. fig. 2. *Agrotis fatidica* (Hübner, 1824)

Gen. fig. 3. *Agrotis proverai* Zilli, Fibiger, Ronkay & Yela, 2010

Gen. figs 1–3. 1–2 *Agrotis fatidica*, male genitalia, **3** *Agrotis proverai*, male genitalia, paratype.

The neotype is a male and bears the following labels: "AUSTRIA occ. | Nordtirol | Rettenbachtal | 2700 m, 5.9.1991 | leg. Burmann et al."; "BC TLMF Lep 00184" (green label). The neotype and its labels are illustrated in Figs 1–2.

Apart from the Alps, published records of *A. fatidica*-like taxa have come from the Pyrenees, the Balkan Peninsula (Albania, Macedonia and Bulgaria) and the Caucasus region. Furthermore, two old specimens from the Frivaldszky collection (HNHM), labelled as "Corsica", are practically identical with those of the specimens from the French and Ligurian Alps. The report of "*A. fatidica*" from Corsica is probably based on these, almost certainly mislabelled, specimens, and the occurrence of a *fatidica*-group species in the island of Corsica has never been confirmed (cf. Brusseaux and Nel 2004).

Von Mentzer and Moberg (1987) excluded the presence of *A. fatidica* from the Ural region; however, the *A. fatidica* specimen illustrated in Noctuidae Europaeae 1: pl. 7, fig. 2, (Fibiger 1991) is from the Urals. Moreover, an allied species, *A. iremeli*, is present in that region.

Agrotis fatidica var. *monedula* is just an individual, dark form from the Ortler Region (South Tyrol) and has no taxonomic relevance. Contrary to the statement of Poole (1989), the type-locality is mentioned in the description.

Agrotis incurva, a junior synonym of *A. fatidica,* was described from three highly variably coloured and shaped females and an unstated number of males collected on the high peaks of the Tyrolean Alps by Stenz (Herrich-Schäffer 1852). In the original description, brachyptery in the female sex was considered as probably the result of malformation.

It remains unclear as to whether some or all the eastern European and Asiatic populations currently referred to *A. fatidica*, either named (e.g. *bombycia* Eversmann, 1851; possibly also *sajana* Corti, 1932) or unnamed (e.g. the Balkanic, Caucasian and Tibetan populations), are actually conspecific with the Alpine ones or not. Material from the Altai Mts which corresponds with *A. fatidica* in external morphology falls within the range of intraspecific DNA barcode variation and is therefore considered as conspecific. However, the barcodes of certain *Agrotis* specimens, identified by their external features as *A. trifurcula* (Staudinger, 1892) and *A. ruta* (Eversmann, 1851), show no divergence from the barcodes of the European populations of *A. fatidica* (see also under *A. trifurcula* and *A. patula*).

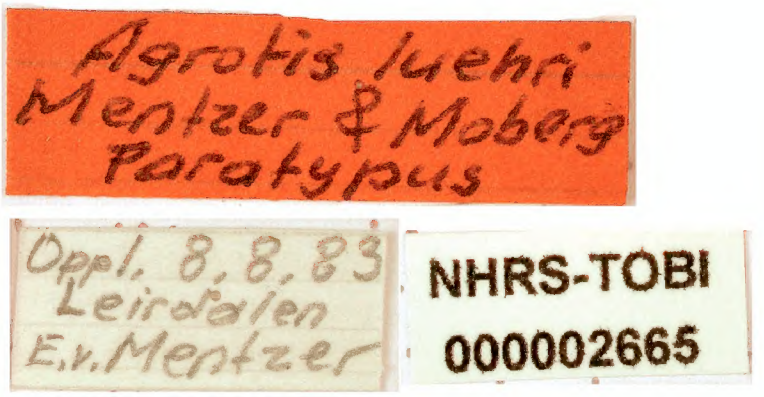
Clearly, subspecific division of *A. fatidica* requires further study, especially with respect to the south-eastern and eastern European populations which are poorly represented in collections.

Agrotis fatidica luehri von Mentzer & Moberg, 1987

Figs 9–16

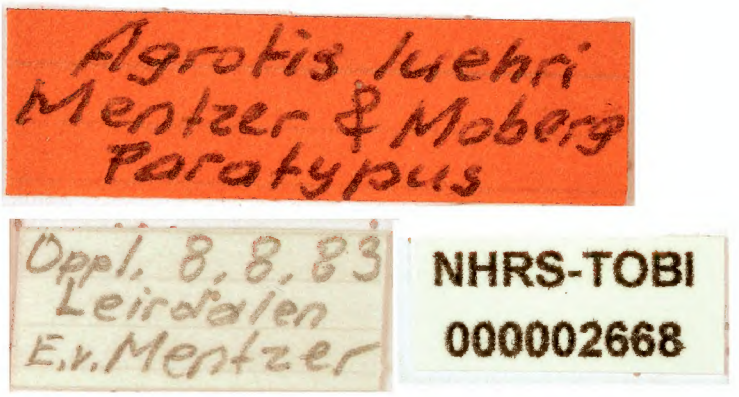
Originally, *A. luehri* was considered to be the Arctic sister-species of *A. fatidica* in which the male has shorter and broader-based lamellae of the antenna, and the female is longer-winged and with thinner antennomeres. It was described from Norway and compared with a long series of "*A. fatidica*" specimens from both Norway and the Alps (von Mentzer and Moberg 1987). Subsequently, however, all Norwegian populations of "*A. fatidica*" were said to represent *A. luehri* (Fibiger 1997, in Noctuidae Europaeae 3: 81). This situation is questionable as it implies that the latter has been diagnosed also in comparison to itself. The distinction of *A. luehri* from the alpine *A. fatidica* was accepted by Fibiger et al. (2010) on the basis of the characters noted above, but the logical incongruence relating to the Norwegian populations can only be explained

9. *Agrotis fatidica luehri* von Mentzer & Moberg, 1987 Paratype male



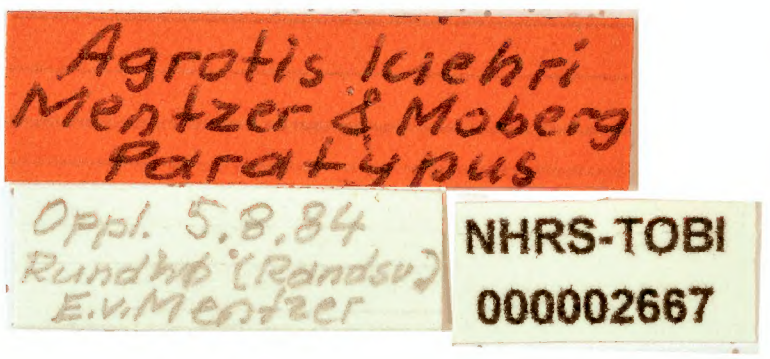
10. *Agrotis fatidica luehri* von Mentzer & Moberg, 1987 Paratype male, labels

11. *Agrotis fatidica luehri* von Mentzer & Moberg, 1987 Paratype male



12. *Agrotis fatidica luehri* von Mentzer & Moberg, 1987 Paratype male, labels

13. *Agrotis fatidica luehri* von Mentzer & Moberg, 1987 Paratype male



14. *Agrotis fatidica luehri* von Mentzer & Moberg, 1987 Paratype male, labels

15. *Agrotis fatidica luehri* von Mentzer & Moberg, 1987 female

16. *Agrotis fatidica luehri* von Mentzer & Moberg, 1987 female, label

Figures 9–16. *Agrotis fatidica luehri*. **1–6** paratype males, Norway, **7–8** female, Norway.

by admitting in *A. luehri* a broader range of variation in morphological characters than that fixed in the original description.

The DNA barcode of 3 specimens from Norway show, however, no difference compared with those of 12 specimens from the eastern Alps (see Table 1). As it seems unlikely that two species occur together in Norway, we consider all the DNA barcodes to be sequences of *A. luehri*. There is some variation in DNA barcodes of *A. fatidica* (within some 0.4%), but the three known DNA barcodes of *A. luehri* nest within this range, matching exactly those of certain specimens of *A. fatidica* from Austria and Switzerland.

Thus, irrespective of the disputed diagnostic characters in morphology, the COI sequences support the conspecificity of *A. luehri* with *A. fatidica*. The detailed investigation of the Scandinavian specimens show, however, differences in the colouration and the wing shape between the nordic and the alpine populations (the ssp. *luehri* is darker and more unicolorous than the ssp. *fatidica*, especially the hindwings are more dark grey suffused, the melanistic specimens appear more frequently; the forewings of the ssp. *luehri* are narrower and more elongated). These differences and the long and complete isolation of *A. fatidica* and *A. luehri* support their distinction at subspecies level, *A. fatidica luehri* stat. rev. (see also Aarvik et al. 2017).

Agrotis proverai Zilli, Fibiger, Ronkay & Yela, 2010

Figs 17–20; Gen. fig. 3

The taxon is endemic to Central Italy (Abruzzo region; on the massif of Gran Sasso d'Italia), and is the only population of the *A. fatidica* species-group outside of the Alps ever found on the Italian Peninsula. Only males have been collected, and it seems likely that the females of this isolated species are brachypterous, as is the case in several other members of the species-group. The male genitalia and various other structural characters correspond with typical *A. fatidica* and its close relatives. Furthermore, DNA barcodes show a high degree of similarity to typical *A. fatidica* from the Eastern Alps, with only ca. 0.5% divergence (n=2), and they belong to the same BIN. The genetic distance from *A. mayrorum* and *A. mazeli* is much greater, minimally 1.55% and 1.71%, respectively.

The habitus of the moths from the Abruzzi region (especially the narrower forewings and the stronger and more prominent noctuid pattern), some allometric differences, and some incongruence in the variation of colours between areas of forewing compared with *A. fatidica* and *A. mayrorum* from the Alps, indicate that the Central Italian population has differentiated sufficiently to qualify as a distinct species.

Agrotis mayrorum sp. n.

Figs 21–32; Gen. figs 4–7, 17

Certain features of the SW Alpine (and the two "Corsican") specimens, distinguish them from the typical eastern Alpine *A. fatidica*, as well as from the *A. characteristica* species-complex and *A. trifurcula*. The main diagnostic features are the proportionally longer and slenderer branches of the male antenna, the pale hindwing of the individuals, the enhanced pale lining of the cubital vein of forewing, the generally obsolete postmedial line, and the somewhat shiny flat, not fluffy scaling. These features are partly shared with examples from Bulgaria and specimens of *A. mazeli* from the

17. *Agrotis proverai* Zilli, Fibiger, Ronkay & Yela, 2010 Paratype male

18. *Agrotis proverai* Zilli, Fibiger, Ronkay & Yela, 2010 Paratype male, labels

19. *Agrotis proverai* Zilli, Fibiger, Ronkay & Yela, 2010 Paratype male

20. *Agrotis proverai* Zilli, Fibiger, Ronkay & Yela, 2010 Paratype male, labels

21. *Agrotis mayrorum* **sp. n.** Holotype male

22. *Agrotis mayrorum* **sp. n.** Holotype male, labels

23. *Agrotis mayrorum* **sp. n.** Paratype male

24. *Agrotis mayrorum* **sp. n.** Paratype male, labels

Figures 17–24. 17–20 *Agrotis proverai*, paratype males, Italy, Abbruzzo region; **21–24** *Agrotis mayrorum*, **21–22** holotype male, Italy, **23–24** paratype male, Italy.

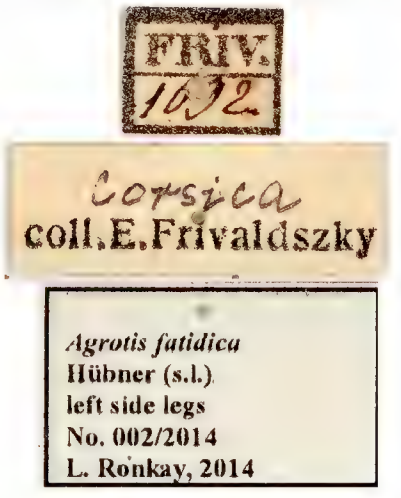
25. *Agrotis mayrorum* **sp. n.** Paratype male

26. *Agrotis mayrorum* **sp. n.** Paratype male, labels

27. *Agrotis mayrorum* **sp. n.** Paratype male

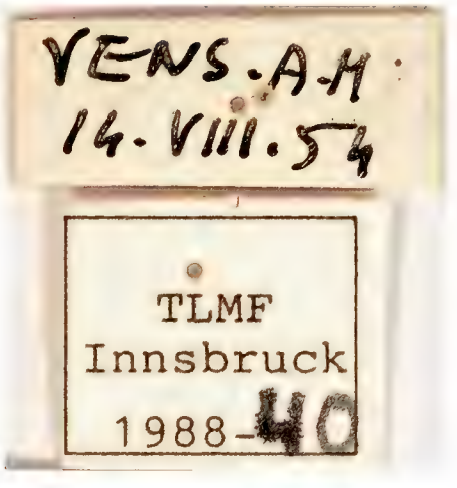
28. *Agrotis mayrorum* **sp. n.** Paratype male, labels

29. *Agrotis mayrorum* **sp. n.** male



30. *Agrotis mayrorum* **sp. n.** male, labels

31. *Agrotis mayrorum* **sp. n.** Paratype female



32. *Agrotis mayrorum* **sp. n.** Paratype female, labels

Figures 25–32. *Agrotis mayrorum*. **25–28** paratype males, France, **29–30** male, "Corsica", **31–32** paratype female, France.

NE Pyrenees, while the *fatidica*-like moths occurring in the Ural region have generally dark hindwings, and their forewing pattern also resemble more closely the typical eastern Alpine *A. fatidica*.

In the male genitalia, the valvae of *A. mayrorum* are comparatively the longest and narrowest within the European species of the *fatidica* complex, having a less dilated distal section, only slightly convex distal dorsal margin and reduced membranous ventral edge along the sacculus. The clasper (harpe) is short and broad, being distinctively shorter than in *A. mazeli* and on average shorter and apically more rounded than in *A. fatidica*; the juxta is also somewhat larger and broader, more pentagonal than in *A. fatidica* and *A. proverai*; and the dentated plate of the phallus is stronger and more densely spiny in *A. mayrorum* than in the related species.

The female genitalia of *A. mayrorum* has, in comparison with *A. fatidica*, proportionally a longer ovipositor, longer apophyses anteriores and a longer appendix bursae; while the ovipositor, the ductus bursae, and the appendix bursae are proportionally longer than in *A. mazeli*.

The species status is strongly supported by genetic distances from other taxa of the *A. fatidica* species-group (see below).

Agrotis sp. near *A. mayrorum* sp. n.

The isolated populations occurring in the high mountains of the Balkans in Bulgaria, Macedonia and Albania appear from their external morphological features to be more similar to the south-western Alpine *A. mayrorum* than to the geographically closer eastern Alpine *A. fatidica*.

The few specimens known from the Caucasus (Daghestan) show transitional features, with rather long branches of the male antennae and greyish suffused but still paler hindwing than in the typical *A. fatidica* populations.

The detailed taxonomic analysis of these populations and their biogeographical constraints requires further research and we cannot identify them with confidence as *A. mayrorum*.

Agrotis mazeli sp. n.

Figs 33–40; Gen. figs 8–9, 18

The Pyrenean populations represent a common lineage with the SW Alpine *A. mayrorum*, sharing the features of the male antennae and the paler (generally white or whitish) hindwing which distinguish the two new species from *A. fatidica*. The specific differences between *A. mayrorum* and *A. mazeli* can be found in the wing shape, the different form of the postmedial line, the shape and size of the dark dots following the terminal line and the colouration of the forewing underside. These are the same characters in which *A. mayrorum* and *A. fatidica* differ (besides the group features mentioned above).

The male genitalia of *A. mazeli* differ from those of *A. fatidica* and *A. mayrorum* by the short and basally broad valvae with the very typical, wide membranous ventral marginal section bordering the saccular part. The cucullus is broad with a finely pointed apex, the clasper (harpe) is rather long and slender, and the dentate subbasal plate of the vesica is weaker than in the closely related European taxa.

The female genitalia of *A. mazeli* have longer apophyses anteriores and a somewhat shorter appendix bursae than those of *A. fatidica*; the ovipositor and the ductus bursae are proportionally shorter, and the appendix bursae is shorter in *A. mazeli* than in *A. mayrorum*.

The species status is strongly supported by genetic distances from other taxa of the *A. fatidica* species-group (see below).

Agrotis trifurcula (Staudinger, 1892)

Figs 41–46; Gen. figs 10–11

The species was described from Mongolia; it is widespread and locally common in Central Asia. Certain authors synonymised it with *A. fatidica* (see e.g. Poole 1989), despite the clearly recognisable differences in the external and genital morphology (see the Figs 1–8, 41–46; Gen. figs 1–2, 10–11). The species has not been treated in detail in the European literature. Some of the last catalogues (Fibiger 1990, 1997; Fibiger et al. 2010; Witt and Ronkay 2012) consider it as a distinct species while Kononenko (2005, Noctuidae Sibiricae Vol. 1) and a recent monograph about the Noctuidae fauna of the western Altai Mts (Volynkin 2012) mention it as *A. fatidica*.

Our investigations on the DNA barcodes of certain *Agrotis* species occurring in the Altai Mts showed, surprisingly, no genetic distance between *A. trifurcula* and *A. fatidica*, indicating possible introgression (Huemer et al. 2017).

Agrotis innocens (Boursin, 1967)

Figs 47–50; Gen. fig. 12

This taxon was described by Boursin from three male specimens collected in the central region of Mongolia by Dr. Z. Kaszab. The specimens of this short series differ conspicuously from the sympatrically occurring and widespread *A. trifurcula* by their pinkish-shaded pale ochreous-grey ground colour of both wings and the reduced pattern.

The genitalia differences between the holotype of *A. innocens* (see Boursin 1967) and the studied specimens of *A. trifurcula* were subtle in the original study since the everted vesica of the two taxa were not examined. The lack of the female and the absence of *A. innocens* in the large samples of *A. trifurcula* from various places of Mongolia and the surrounding areas implied the possible conspecificity of the two taxa, especially as there are no remarkable differences in the male antennal characters. The study of the vesica of the two species revealed notable differences in the configuration of the vesica. The vesica of *A. innocens* is clearly longer than that of *A. trifurcula*, medially slightly dilated and distally evenly tapering, and is without a thickening at the nearby ductus ejaculatorius, which is typical of *A. trifurcula* (see the Gen. figs 10–12). Thus, *A. innocens* is considered here as a species distinct from *A. trifurcula*.

Agrotis characteristica Alphéraky, 1892/*Agrotis robusta* Eversmann, 1856 nec Blanchard, 1852 (= *robustana* Poole, 1989)

Gen. fig. 15

After over a century of confusion regarding the identity of *A. characteristica* and *A. robusta*, and of these with other taxa of the *A. fatidica* species-group (e.g. *trifurcula* Staudinger, 1892, *sajana* Corti, 1932) (Corti 1932 in Corti and Draudt 1931–1933; Kozhanchikov 1937; von Mentzer and Moberg 1987), these two names were recently synonymised, thus making *robustana* Poole an unnecessary replacement name for *robusta* Eversmann, preoccupied by Blanchard (see Kononenko et al. 1998; Kononenko 2005). Nevertheless, there is evidence that two concepts are still mixed under *A. characteristica*: that adopted by Fibiger (1990: pl. 1) in Noctuidae Europaeae Vol. 1., referring to a form with comparatively short lamellae in the male antenna and non-brachypterous females

which occurs in the Urals, and an Asiatic insect, referred to by Kononenko et al. (1998), which has longer lamellae, and fully-winged females. In passing, it may be noted that Corti (1931–1933: pl. 5, row l) illustrated a brachypterous female of "*A. robusta*" while stating in the text that the female is fully developed and larger than the male. Unfortunately, the type specimen of *characteristica* is a female, which prevents an undisputed morphological assessment of its relationship to *robusta*. On the other hand, it seems likely that these two names may actually refer to the same Asiatic species, as their type localities suggest ([Inner Mongolia]: Ordos and Southern Altai, respectively). If so, the populations of the "Ural form" still remained unnamed.

Agrotis iremeli Nupponen, Ahola & Kullberg, 2001

As a close relative of *Agrotis ruta* (Eversmann, 1851), this species is also a member of the *A. fatidica* species-group which, on grounds of larval morphology, reveals a relationship with the *A. segetum* ([Denis & Schiffermüller], 1775) species-group, notably *A. clavis* (Hufnagel, 1766) (Nupponen et al. 2001). The large size and the dark reddish-brown ground colour of *A. iremeli* make it unlikely to be confused with its congeners. It is most like *A. ruta*, the ground colour of which is however always grey and less monotonous, more mottled with darker and paler areas, and has darker, more sharply defined stigmata, and a more wedged subterminal line. Some forms of *A. cinerea* ([Denis & Schiffermüller], 1775) might be mistaken for *A. iremeli*, particularly some females, but as a rule they are smaller, with more weakly crenulated antemedial line of forewing, absolutely tiny orbicular stigma, if any, smaller reniform and no claviform.

A. iremeli has been collected solely in restricted biotopes with xeric, rocky montane tundra, either in clearings within taiga forest or on the peaks of the mountains of the South Urals, at an altitude of 1300–1400 m. It appears to be endemic to the Southern Urals, in essentially similar habitats of the Northern Urals where only *A. ruta* was found (Fibiger et al 2010, citing K. Nupponen).

Agrotis ruta (Eversmann, 1851)

Figs 51–56; Gen. figs 13–14

The only Holarctic member of the species-group. Its Nearctic populations have long been distinguished under the name *A. patula*. The type-locality of the species is poorly defined ("eastern Siberia"). The species appears to be distributed from the Ural Mountains through Central and eastern Asia to the Pacific area and in vast parts of North America. It is highly variable in external features, with several, often remarkably dissimilar, forms and local populations. Recent molecular studies (Zahiri et al. 2014) show, however, a high consistency within the Canadian populations whereas material from the Altai Mts is distant and clusters nearest to *A. proverai*. Further in depth studies are necessary for the Palaearctic populations.

Agrotis patula (Walker, 1857)

The species was described from the Rocky Mountains (USA), but several large European collections house specimens under this name from Labrador and from the eastern side of the mountains of North America (named by Möschler as *A. septentrionalis* in 1862) and from the northern part of Pacific Asia (Japan: *"Euxoa" kurodakeana* Matsumura, 1927; Russia, Kurili Islands: *Feltia*

Table 2. Intraspecific mean K2P (Kimura 2 parameter) divergences, maximum pairwise distances, and distance to the nearest neighbour in the *Agrotis fatidica* species-group.

	A. fatidica	***A. proverai***	***A. mazeli***	***A. mayrorum***
n	15	2	3	5
BIN	BOLD:AAA1629	BOLD:AAA1629	BOLD:ACR9899	BOLD:ACE4355
average distance	0.18% (p-dist)	0% (p-dist)	0% (p-dist)	0% (p-dist)
maximum distance	0.51% (p-dist)	0% (p-dist)	0% (p-dist)	0% (p-dist)
distance NN	0.48% (p-dist)	0.48% (p-dist)	1.12% (p-dist)	1.12% (p-dist)
NN	*A. proverai*	*A. fatidica*	*A. mayrorum*	*A. mazeli*

subinformis Bryk, 1941). All these taxa have been recently considered to represent a single species, *A. ruta* (Kononenko 2005; Lafontaine and Schmidt 2010), mainly due to their very similar DNA barcodes. The fact that the DNA barcodes of certain closely related taxa of the *A. fatidica* group (e.g. *A. trifurcula* and *A. ruta*) are identical or very similar suggests that the *ruta–patula* complex needs to be reviewed.

Agrotis xylographa Boursin, 1948

The species was described from a single male specimen from Transbaikalia when our knowledge of the *fatidica*-group species was limited. At that time, separation of *A. xylographa* from *A. ruta* seemed reasonable. Subsequent study based on much more material of *ruta* shows the great external variation of the Asiatic populations of *A. ruta* (s. str.), as well as its wide range from the Ural region throughout Siberia and Mongolia to the Pacific area. The holotype of *A. xylographa* falls within the morphological and geographical range of *A. ruta*. Accepting the statement by Kononenko (1990; 2005), we treat *A. xylographa* as a junior synonym of *A. ruta*. *Agrotis xylographa* does, however, differ from the Asian Pacific specimens of *A. "patula"*.

Molecular results

25 specimens belonging to 4 species were successfully sequenced (Table 1) and group in 4 different clades (Fig. 61). Maximum intraspecific distances are ranging between 0% and 0.51% whereas minimum distances to the nearest neighbour are between 0.46% and 1.12% (Table 2). *Agrotis mazeli* sp. n. and *A. mayrorum* sp. n. have unique BINs (Barcode Index Number) in BOLD (Ratnasingham and Hebert 2013), whereas *A. fatidica* and *A. proverai* share their BIN.

Description of the new species

Agrotis mayrorum sp. n.

http://zoobank.org/4717ACCD-4279-435E-B937-B1964DF13F19

Figs 21–32; Gen. figs 4–7, 17

Holotype. Male, Italy, Prov. Cuneo, Alpi Cozie, Demonte NW, Colle Valcavera NE, 2420 m, 17.VIII.2012, leg. P. Huemer; DNA Barcode ID TLMF Lep 08820 (TLMF).

Paratypes. Italy. 15 males, Prov. Cuneo, Alpi Cozie, Demonte NW, Colle Valcavera NE, 2420 m, 17.viii.2012, leg. P. Huemer; slide No. RL11122m; DNA Barcode IDs TLMF Lep 08647, TLMF Lep 08648,

TLMF Lep 08819 (TLMF); 2 males, Prov. Cuneo, Alpi Cozie, Demonte NW, Colle Valcavera, 2450 m, N 44°22,9', E 07°07,2', 16.viii.2013, leg. Mayr (RCTM); 10 males, Prov. Cuneo, Alpi Cozie, Demonte NW, Gias Valcavera, 2050 m, N 44°22,6', E 07°08,2', 17.viii.2012, leg. Mayr; slide No. P. Huemer N 1591♂ (RCTM; TLMF); 2 males, Prov. Cuneo, Alpi Cozie, Demonte NW, Gias Valcavera, 2050 m, N 44°22,6', E 07°08,2', 16.viii.2013, leg. Mayr (RCTM); 4 males, Prov. Cuneo, Alpi Cozie, Demonte NW, Gias Valcavera, 2050 m, N 44°22,6', E 07°08,2', 28.vii.2015, leg. Mayr (RCTM). **France**. 1 male, Alpes Maritimes, Colle di Tenda, Fort Central Alpi Marittimi, 1870 m, 6.viii.1996, leg. A. Otter; slide No. RL11123m (TLMF); 1 female, Alpes Maritimes, Vens, 14.viii.1954, slide No. RL11780f (TLMF); 2 males, Alpes Maritimes, Col de la Bonette, 2100 m, 14.viii.1977, leg. F. Dujardin (TLMF); 2 males, Alpes Maritimes, Col de la Bonette, 2100 m, 21.viii.1977, leg. F. Dujardin (TLMF); 2 males, Alpes Maritimes, Col de la Bonette, 2800 m, 27.viii.1978, leg. F. Dujardin (TLMF); 2 males, Basses-Alpes, Larche, Harold Powell, 1-27.viii.1918, ex coll. Oberthür, slide No. RL11513m (BMNH); 1 male, Larche, ex coll. Bellier, slide No. RL11514m (BMNH); 1 male, Basses Alpes, Larche, Aout 1897, 3 Coulet, coll. Oberthür (BMNH); 2 males, „Larche, ex coll. Oberthür" (BMNH); 1 male, Hautes Alpes, Col de la Cayolle, 2326 m, 29.–30.vii.2009, leg. B. Skule; DNA Barcode ID TLMF Lep 16460 (RCBS); 1 male, Hautes Alpes, col de Vars, 2115 m, 31.vii.–7.viii.1933, leg. Ch. Boursin (BMNH); 1 male, Hautes Alpes, St. Veran, viii.1929, coll. Stempffer (ZMHU); 2 males, Basses Alpes, Col de Restefond, 15.viii.1990, leg. E. von Mentzer, slide No. 13098; NRMS TOBI 00194, 00198 (NRMS).

Etymology. Named in honour of Marlies and Toni Mayr (Feldkirch, Austria) who collected the new species in companionship with Peter Huemer and recognized its differing morphology.

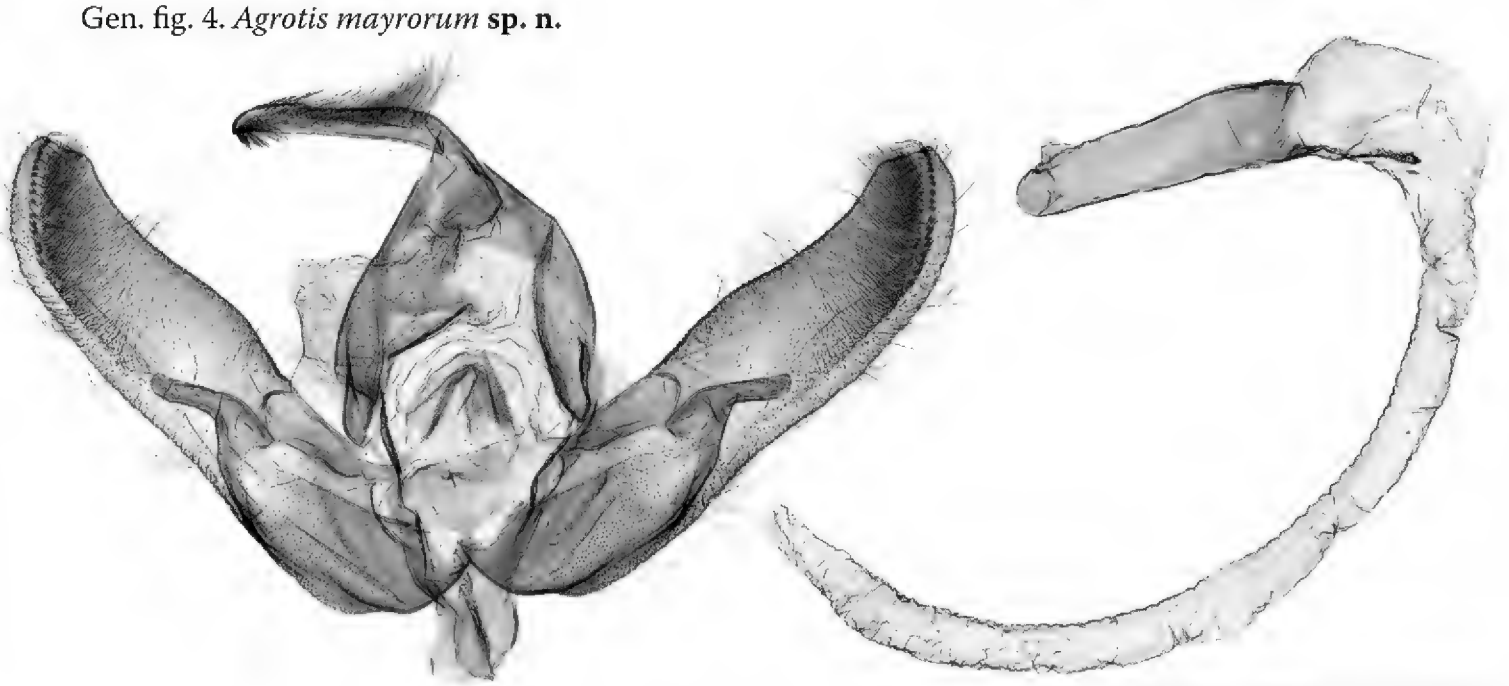
Diagnosis. The new species can be distinguished from the pale forms of *A. fatidica* by its lighter appearance, which is the consequence of the generally paler, milky whitish hindwings. The hindwings of the new species have only sparse, light greyish-brown irroration along the costal margin and narrow and discontinuous submarginal stripe while the narrow marginal ribbon along the variably dark, often obsolescent or deleted terminal line is whitish, as are the hindwing cilia. The discal lunule is just a fine shadow on the upperside, and the veins have a fine brownish covering. The underside of the hindwing lacks the transverse stripe (only a diffuse patch at costal margin may be present), the costal area is paler, suffused with brown, and the discal spot is rather weak, usually with a whitish inner liner on the crossvein of the cell.

By contrast, in *A. fatidica*, the typical specimens have dark greyish-brown suffused hindwings, with variably strongly diluted inner area, and a more prominently marked discal spot. Specimens with paler hindwings are relatively rare, but even they have broader and darker marginal field, extending in almost every specimen to the terminal line, and the discal lunule is stronger and darker, more contrasting than in *A. mayrorum*. The hindwing underside of *A. fatidica* is generally darker, usually with a broad and diffuse transverse stripe and a darker discal spot; these elements of the underside pattern are more strongly marked even in the palest *A. fatidica* specimens than in the new species. Another typical feature of *A. mayrorum* is the diffuse or obsolete postmedial line, which is less curved at the costa than in *A. fatidica* and *A. mazeli*. The dark dots tracking the fine terminal line are less prominent on the upperside than in the other two close relatives, and are almost invisible on the underside, only the thin terminal line is clearly marked. The detailed comparison of *A. mayrorum* and *A. mazeli* is given under the diagnosis of the latter species.

Agrotis mayrorum can easily be distinguished from *A. proverai* by the external features of the moths, being on average remarkably larger, with a more robust body and distinctly broader forewings, paler and more greyish ground colour and more prominent tessellate wing pattern, having

RL11122 Paratype, Italy, Prov. Cuneo

Gen. fig. 4. *Agrotis mayrorum* **sp. n.**



RL11123 Paratype, France, Alpes Maritimes

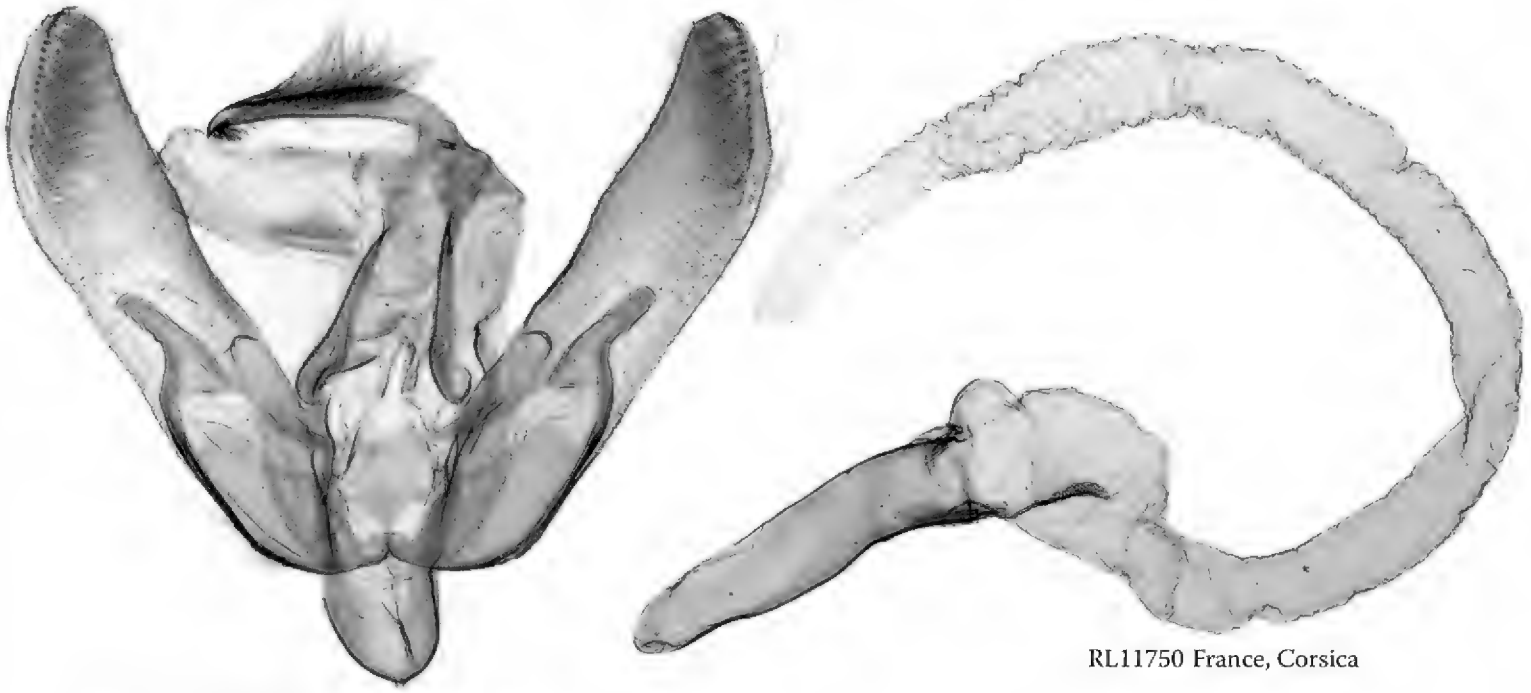
Gen. fig. 5. *Agrotis mayrorum* **sp. n.**

RL11513 Paratype, France, Larche

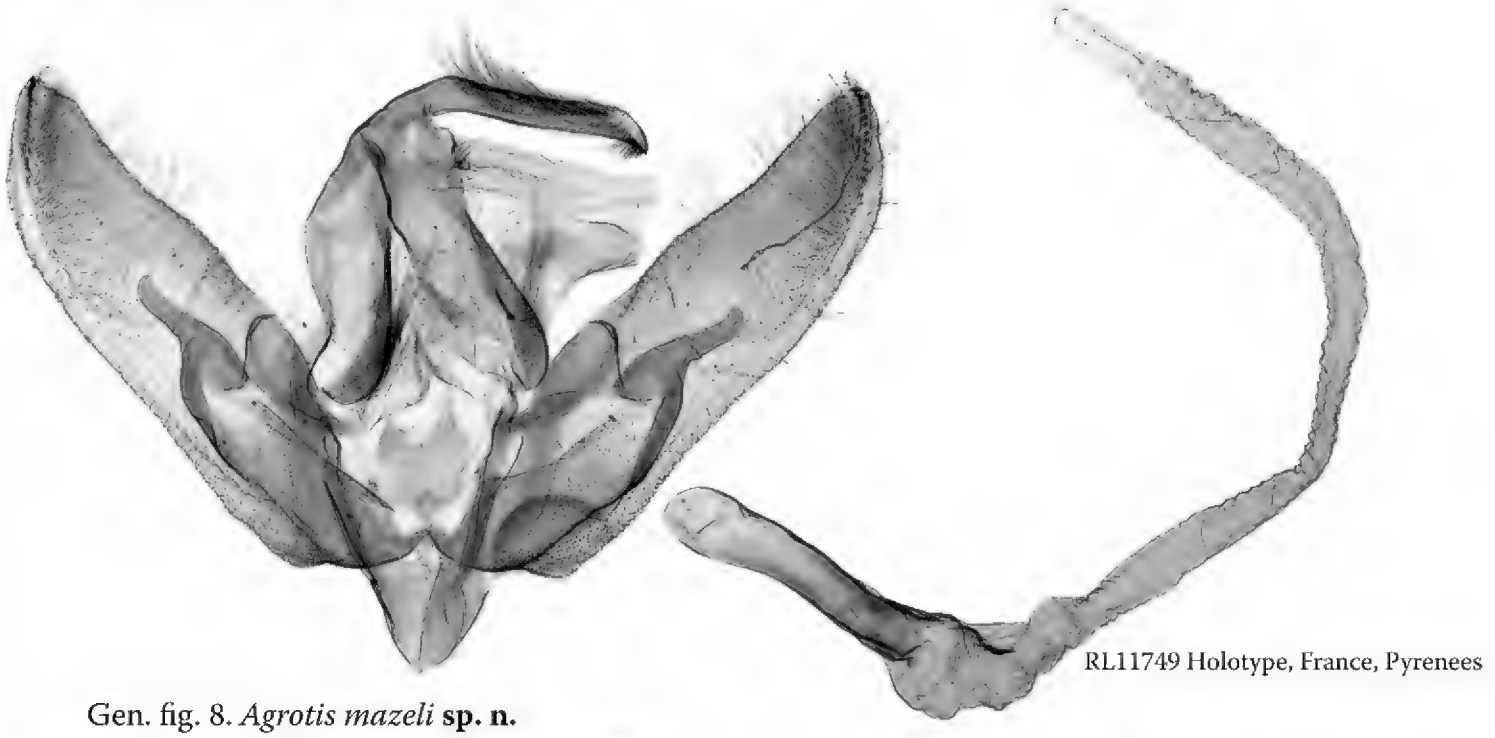
RL11514 Paratype, France, Basses Alpes

Gen. fig. 6. *Agrotis mayrorum* **sp. n.**

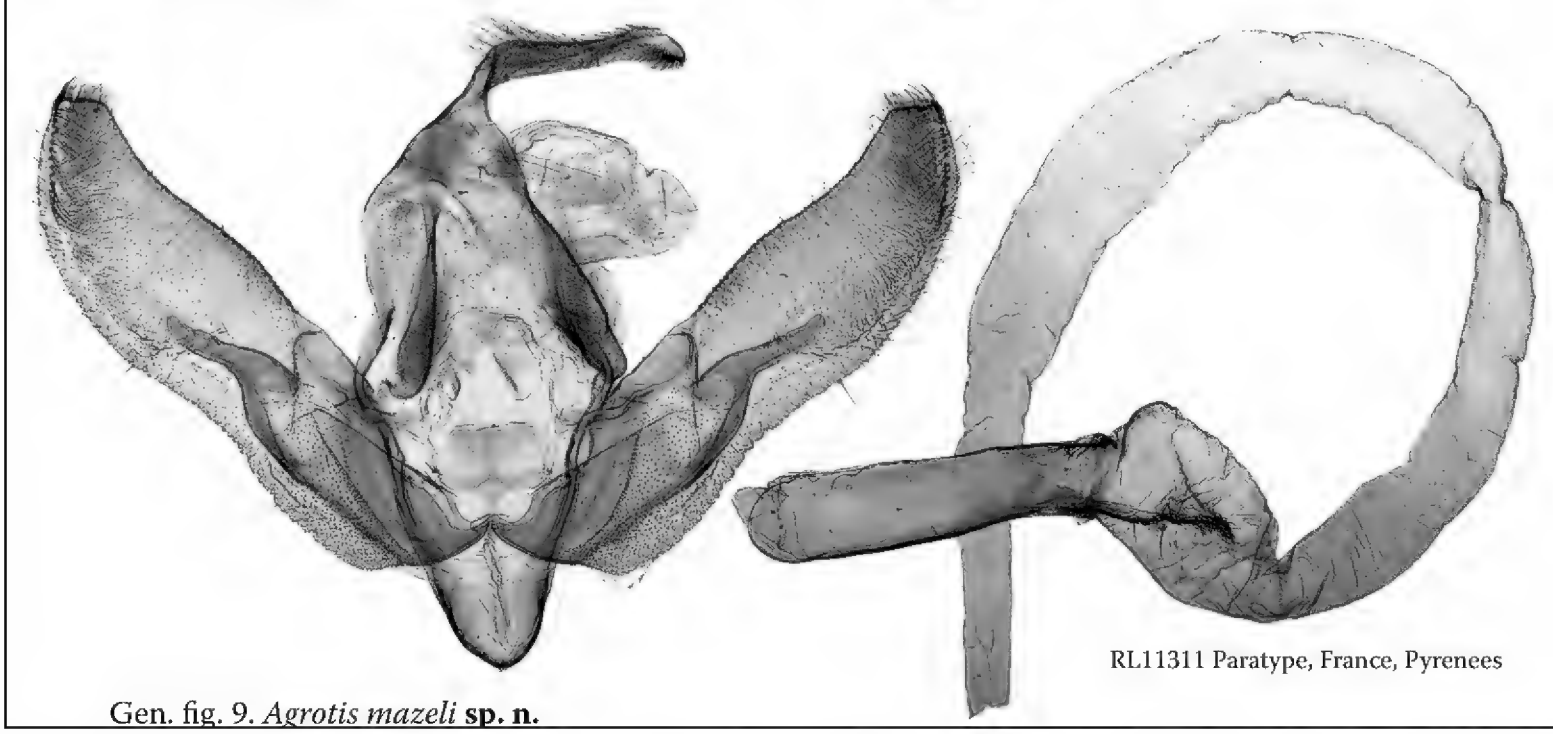
Gen. figs 4–6. *Agrotis mayrorum* sp. n., paratype, male genitalia.



Gen. fig. 7. *Agrotis mayrorum* **sp. n.**



Gen. fig. 8. *Agrotis mazeli* **sp. n.**



Gen. fig. 9. *Agrotis mazeli* **sp. n.**

Gen. figs 7–9. 7 *Agrotis mayrorum* sp. n., male genitalia, „Corsica", **8–9** *Agrotis mazeli* sp. n., male genitalia, **8** holotype, **9** paratype.

characteristically prominent pale lining of the cubital vein and the much paler, never strongly dark filled reniform stigma. The other elements of the wing pattern (e.g. the shape and distinctness of the postmedial line, its distance from the reniform stigma, the shape and size of the arrowhead-spots, etc.) sometimes overlap with the condition in *A. proverai* so are unreliable, although they are usually different in the majority of the specimens.

The frontal prominence of *A. mayrorum*, although somewhat variable in shape and size, is less thick and more rounded or drop-shaped than the taller, more protruding frontal prominence of *A. proverai*.

The diagnostic features of the male genitalia of *A. mayrorum* are the long and slender valva (comparatively the longest and narrowest within the European species of the *fatidica* complex), with a less dilated distal section and only a slightly convex distal dorsal margin and reduced membranous ventral edge along the sacculus; the most often elongated-triangular cucullus with pointed apex; the short and broad clasper, which is distinctly shorter than in *A. mazeli* and on average shorter and apically more rounded than in *A. fatidica*; the juxta is also somewhat larger and broader, more pentagonal than in *A. fatidica* and *A. proverai*. The basal dilated section of the vesica is large with a well-developed, rounded conical dorsal diverticulum; the ventral carinal bar and the subbasal serrate-dentate plate of vesica are connected by an angled membranous part. The carinal bar and the dentated plate are usually directly connected in the other three close relatives and the dentated plate is regularly stronger and more densely spiny in *A. mayrorum* than in the related species.

The female genitalia of the three closely related species are very similar (the female of *A. proverai* is still unknown), although some differences can be found in the length and proportion of the ovipositor, the apophyses anteriores and the appendix bursae. *Agrotis mayrorum* has, in comparison with *A. fatidica*, proportionally a longer and more elongated ovipositor, longer apophyses anteriores and a longer appendix bursae; while the ovipositor, the ductus bursae, and the appendix bursae are proportionally longer than in *A. mazeli*.

Description. Wingspan: males 40–45 mm, female 31 mm. The external appearance of *A. mayrorum* is similar to that of *A. fatidica*, but has narrower, more elongated and somewhat paler coloured forewings and much paler, ochreous-shaded whitish hindwings. Forewing ground colour pale creamy beige, mottled with pale brown and grey; costal area and all veins somewhat darker grey or grey-brown and defined broadly with paler ochreous-grey stripes. Antemedial line indistinct, double, strongest at dark claviform stigma, its lower tooth relatively long. Median fascia absent; median area with a few intracellular dark streaks running from postmedial line to lower cellvein; postmedial line obsolete, appearing as a thin pale shadow defined by a few darker dots between veins. Subterminal line faint, zigzagged, pale ochreous-grey, defined by conspicuous though not very sharply marked chevron-spots; terminal line fine, black(ish), either continuous or divided into a row of fine black lunules and/or streaks; fringe pale creamy beige, occasionally with somewhat darker brown midline. Stigmata well-defined, regularly outlined by black or dark blackish-brown; claviform stigma long, apically faintly rounded, with fine blackish-brown streak connecting it to postmedial line, its filling darker brown; orbicular of variable size and shape, most often flattened-elliptical, sometimes with pointed lateral edges and darker brown centre; reniform stigma large, elliptical, darkened, particularly in its distal half. Intracellular patch between stigmata dark brown or blackish; supracellular marking between crossvein and postmedial line also well-defined, blackish. Hindwing pale whitish or milky-white with fine ochreous sheen, costal area, termen and diffuse marginal stripe suffused with ochreous-brown; veins also brownish.

Discal spot weak, small, often obsolete or missing; terminal line more or less continuous, pale ochreous-brown; cilia whitish or ivory-coloured. Forewing underside ochreous-whitish, variably suffused with pale fuscous, with faint discal dot and postmedial line; hindwing underside whitish with fine ochreous sheen, veins darkened, transversal line absent or very pale, shadow-like; discal spot also indistinct, pale brown with whitish centre.

Molecular data. BIN URI: BOLD: ACE4355. The intraspecific average and maximum distances of the barcode region are 0% (p-dist) (n=5), however intraspecific divergence may increase with additional samples from the Alps. The minimum distance to the nearest neighbour *Agrotis mazeli* is 1.12%, whereas the minimum distance to *Agrotis fatidica* is 1.71%.

Bionomics. Host-plant and early stages are unknown. The adults fly relatively late in the season within a period lasting from late July to mid-August, probably even later. Most of the specimens were obtained by light trapping using both UV tubes and mercury vapour lamp. Adult records are restricted to alpine meadows and scree at high altitudes from ca. 1900 to 2450 m a.s.l. (Figs 57–59).

Distribution. The new species is known from the south-western Alps in Italy (Alpi Cozie) and in France from the Alpes Maritimes and the Alpes-de-Haute-Provence (formerly Basses Alpes, Hautes Alpes).

Agrotis mazeli sp. n.

http://zoobank.org/C7C684FD-D230-479C-B13D-2E7F83EBAE8F

Figs 33–40; Gen. figs 8–9, 18

Holotype. Male, France, Canigou, Pla Guillem, 2280 m, 8.viii.1985, leg. G. Lutran; slide No. RL11749m (TLMF).

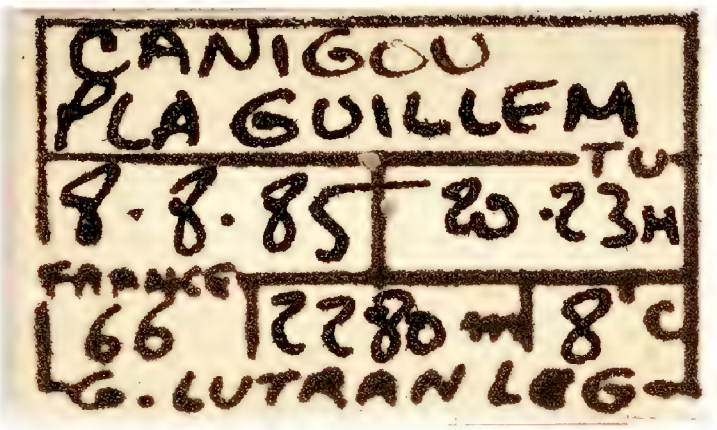
Paratypes. France. 4 males, French Pyrenees orientales, Esquerdes de Rotja, 2200 m, 4.viii.1994, S. Peslier leg.; slide No. RL11311m, DNA Barcode ID TLMF Lep 14494 (TLMF); 1 male, Pyrenees orientales, Pla Guillem, 2.viii.1994, R. Mazel leg., DNA Barcode ID TLMF 14495 (TLMF); 1 female, Pyrenees orientales, Pla Guillem, 8.viii.1994, R. Mazel leg.; slide No. RL11312f (TLMF); 1 male, Pyrenees orientales, Pla de la Begude, 2300 m, 10.viii.1999, R. Mazel leg., DNA Barcode ID TLMF 14496 (TLMF); 1 male, "la Vernet 1879, Vallée Lipaudière, ex coll. Dr. Struve, Leipzig, coll. Püngeler" (see also Struve 1882) (ZMHU).

Etymology. Named in honour of Robert Mazel who collected most of the type-series and generously supported our work with this important material.

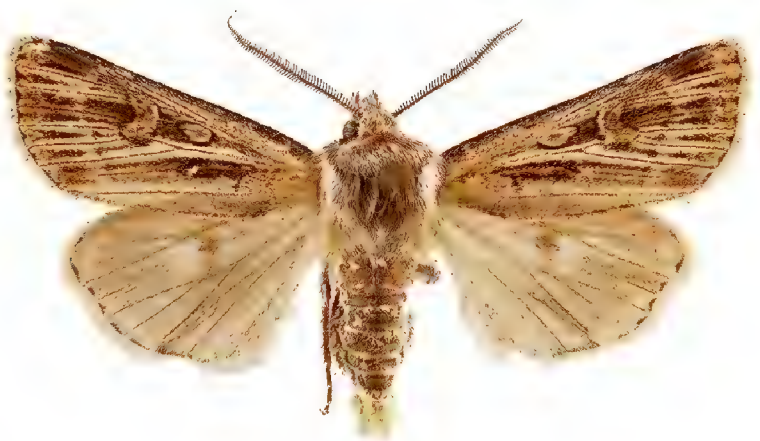
Diagnosis. The new species is the allopatric sister species of *A. mayrorum*, sharing the group features in the male antenna (longer and finer branches than in the *fatidica*-line), and the white (or whitish) hindwing. The two species can be distinguished by a series of external morphological features which are recognisable in almost all specimens. These differences are ca as large as those between *A. mayrorum* and *A. fatidica*.

Agrotis mazeli differs from *A. mayrorum* by its somewhat narrower and more pointed forewings, which are also narrower and apically more pointed than those of *A. fatidica* but broader than those of *A. proverai*, a more sharply defined postmedial line with a clearly visible deep curve inwards at costal margin, on average smaller and more darkened orbicular and reniform stigmata, smaller and finer dark dots at terminal line, which are practically missing from the underside, and the smoothly, rather uniformly darkened forewing underside.

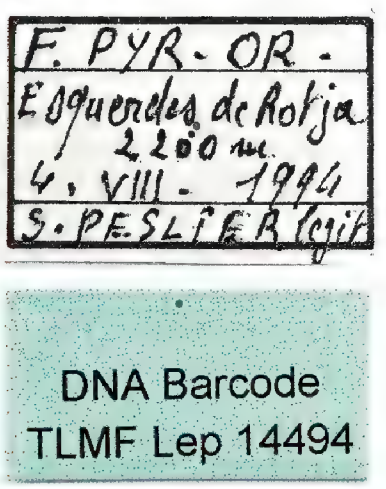
33. *Agrotis mazeli* **sp. n.** Holotype male



34. *Agrotis mazeli* **sp. n.** Holotype male, label

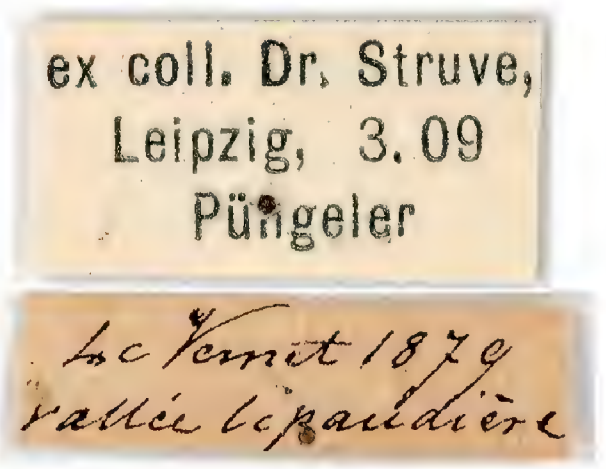


35. *Agrotis mazeli* **sp. n.** Paratype male



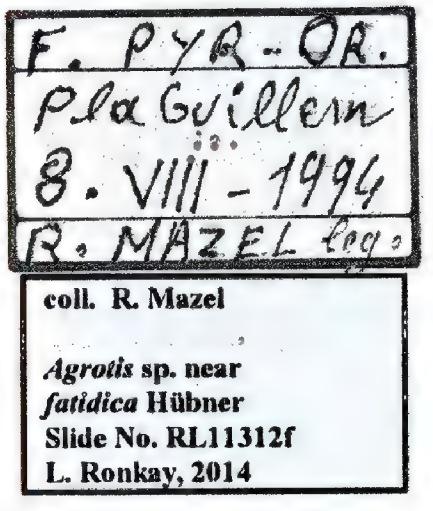
36. *Agrotis mazeli* **sp. n.** Paratype male, labels

37. *Agrotis mazeli* **sp. n.** Paratype male



38. *Agrotis mazeli* **sp. n.** Paratype male, labels

39. *Agrotis mazeli* **sp. n.** Paratype female



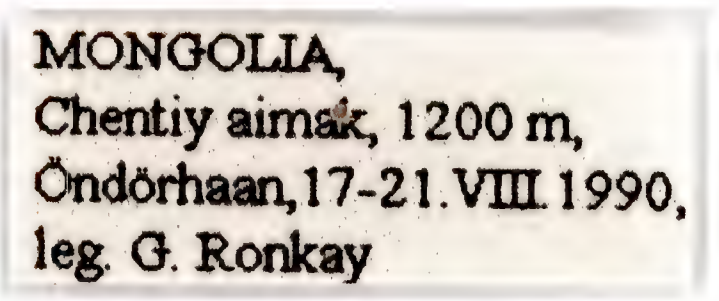
40. *Agrotis mazeli* **sp. n.** Paratype female, labels

Figures 33–40. *Agrotis mazeli*. **33–34** holotype male, France, **35–38** paratype males, France, **39–40** paratype female, France.

41. *Agrotis trifurcula* Staudinger, 1892 Holotype male

42. *Agrotis trifurcula* Staudinger, 1892 Holotype male, labels

43. *Agrotis trifurcula* Staudinger, 1892 male

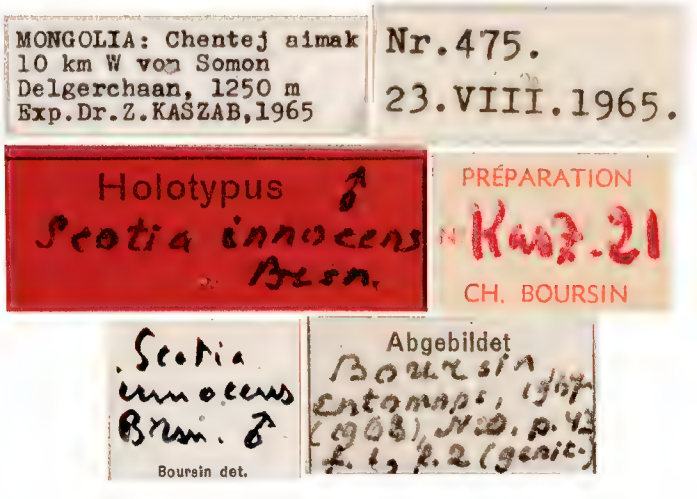


44. *Agrotis trifurcula* Staudinger, 1892 male, label

45. *Agrotis trifurcula* Staudinger, 1892 female

46. *Agrotis trifurcula* Staudinger, 1892 female, label

47. *Agrotis innocens* (Boursin, 1967) Holotype male

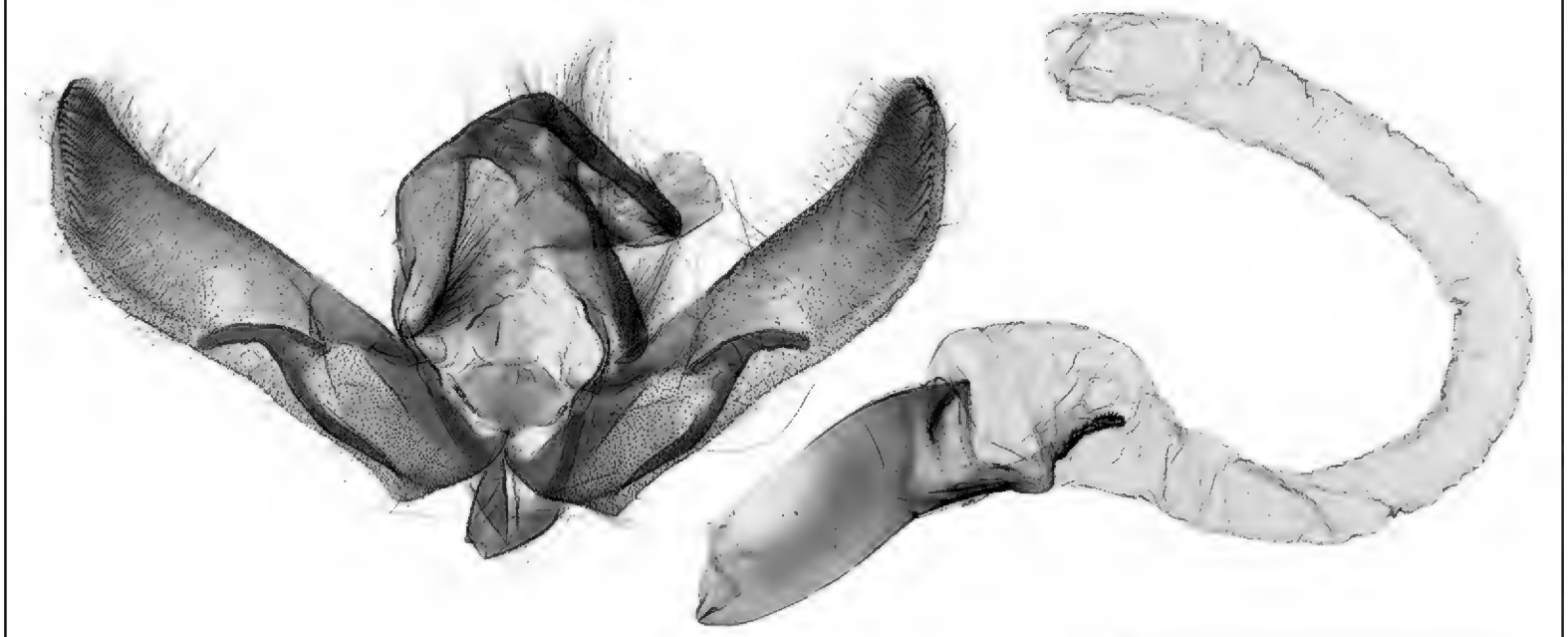


48. *Agrotis innocens* (Boursin, 1967) Holotype male, labels

Figures 41–48. 41–46 *Agrotis trifurcula*, **41–42** holotype male, Mongolia, **43–44** male, Mongolia, **45–46** female, Mongolia; **47–48** *Agrotis innocens*, holotype male, Mongolia.

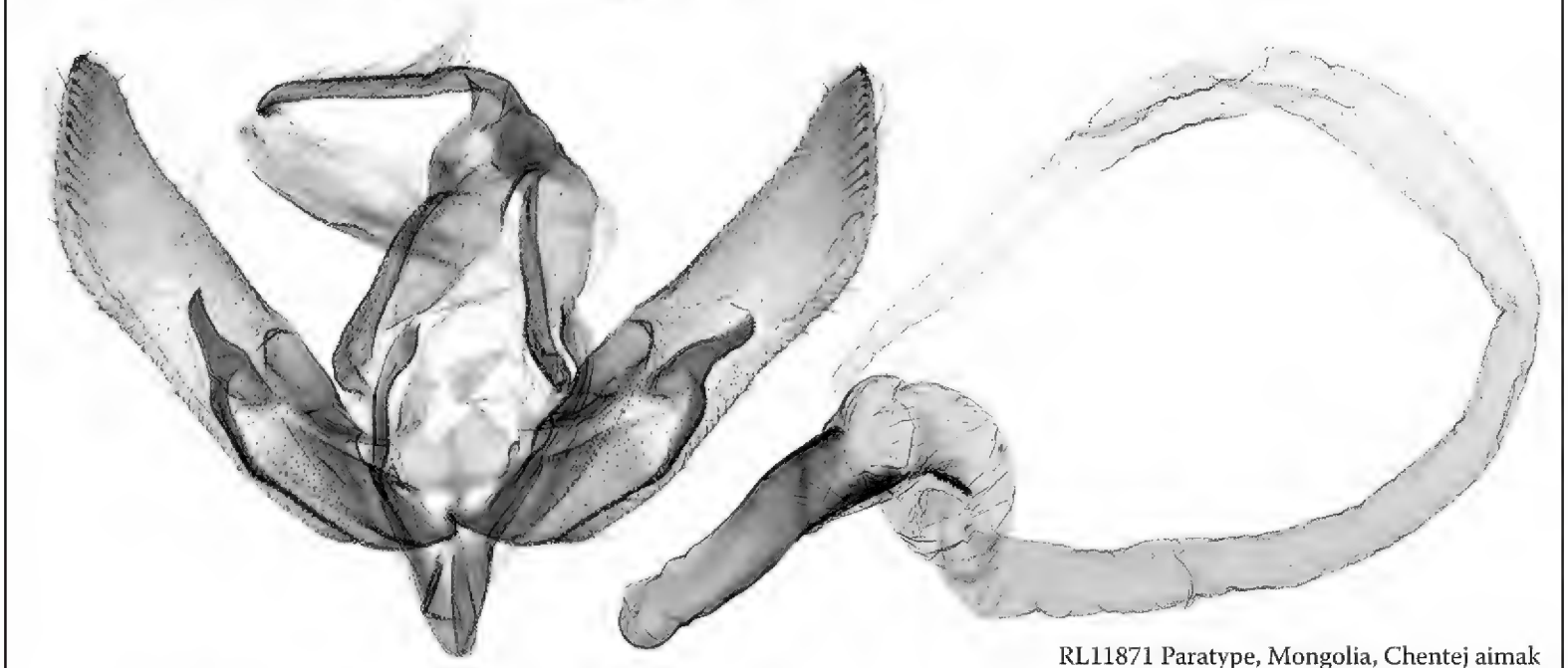
RL11874 Mongolia, Övörkhangay aimak

Gen. fig. 10. *Agrotis trifurcula* Staudinger, 1892



RL11875 Mongolia, Khovd aimak

Gen. fig. 11. *Agrotis trifurcula* Staudinger, 1892



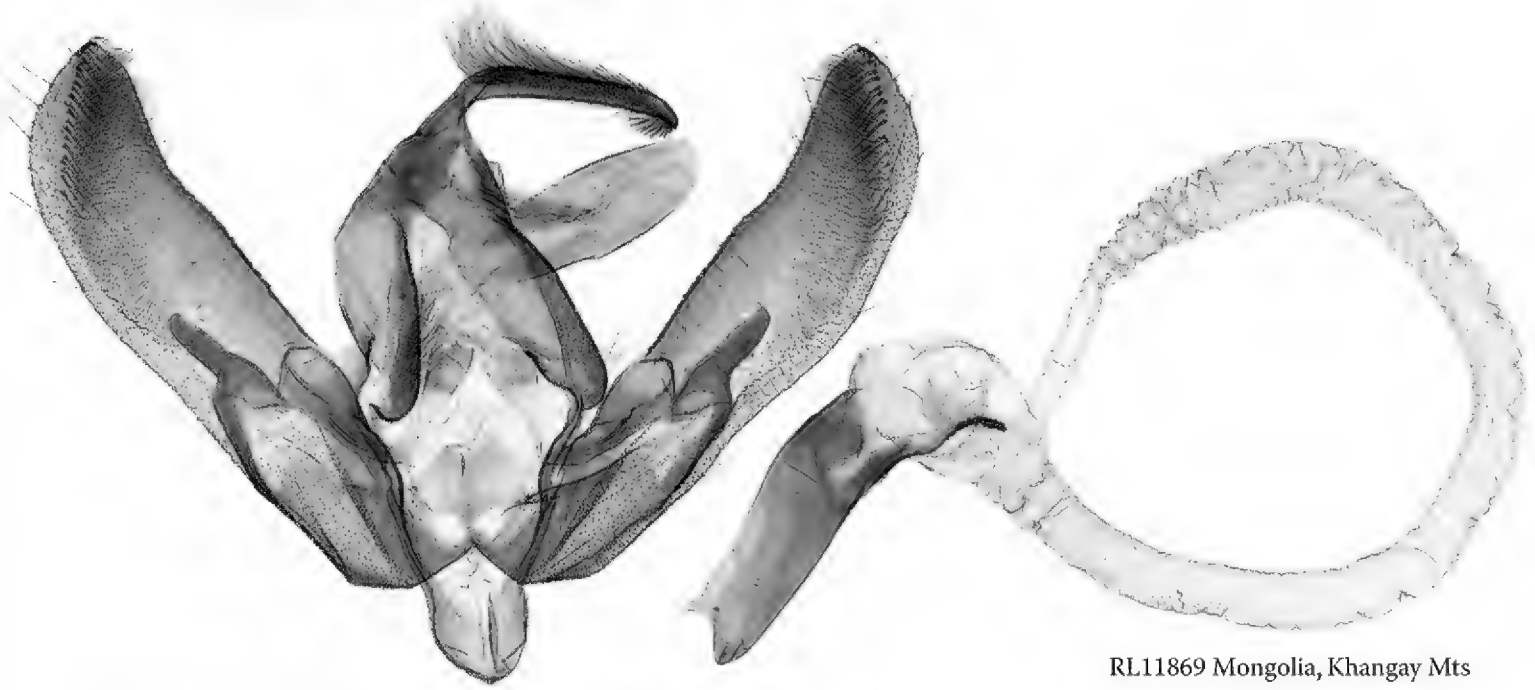
RL11871 Paratype, Mongolia, Chentej aimak

Gen. fig. 12. *Agrotis innocens* Boursin, 1967

Gen. figs 10–12. 10–12 *Agrotis trifurcula*, male genitalia, Mongolia, **12** *Agrotis innocens*, paratype male genitalia, Mongolia.

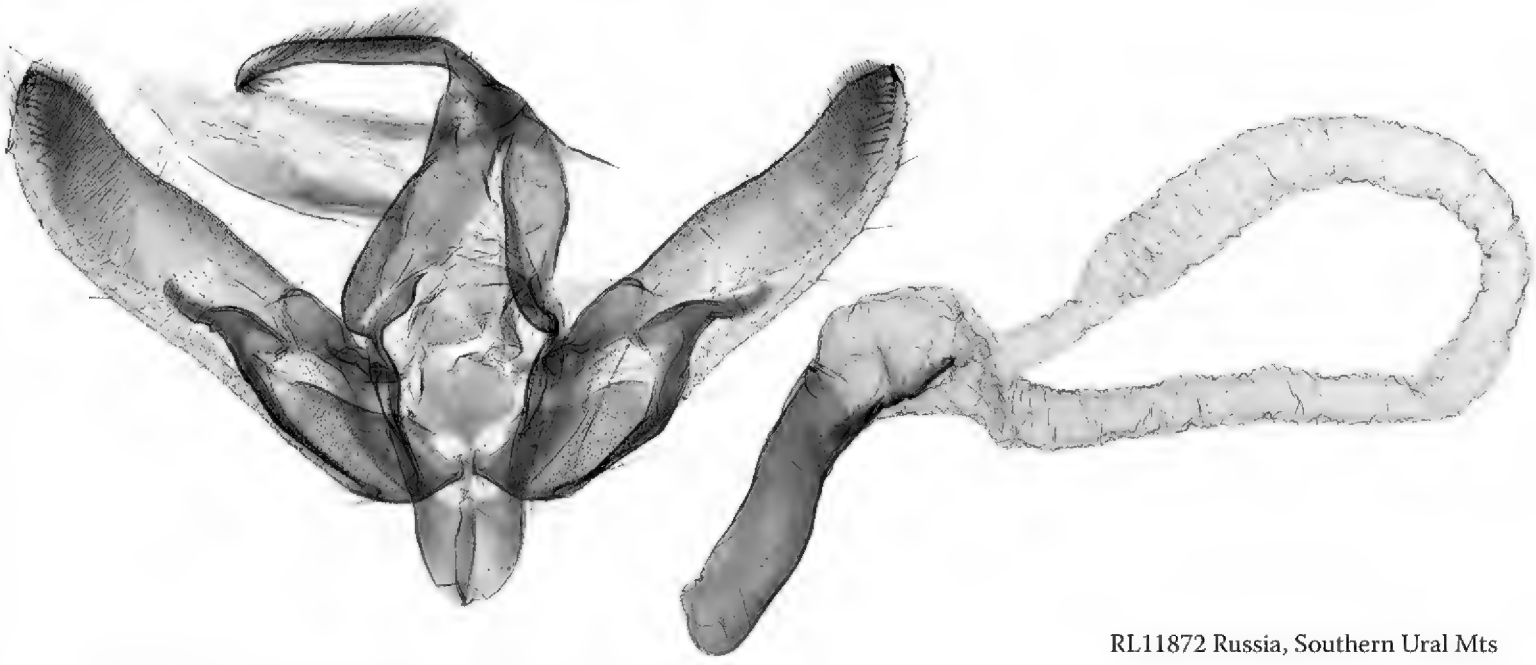
RL11870 Mongolia, Khangay Mts

Gen. fig. 13. *Agrotis ruta* (Eversmann, 1851)



RL11869 Mongolia, Khangay Mts

Gen. fig. 14. *Agrotis ruta* (Eversmann, 1851)



RL11872 Russia, Southern Ural Mts

Gen. fig. 15. *Agrotis characteristica* Alphéraky, 1892

Gen. figs 13–15. 13–14 *Agrotis ruta*, male genitalia, Mongolia, **15** *Agrotis characteristica*, male genitalia, southern Urals.

In the genitalia, the males of *A. mazeli* can be distinguished from those of the closely related taxa by the short and basally broad valvae with the very typical, wide membranous ventral marginal section bordering the saccular part; the broad cucullus with finely pointed apex; the rather long and slender claspers; the comparatively short vinculum; the fine eversible bar of the ventral carina and the weak, dentated subbasal plate of the vesica; the rather short and obtusely conical dorso-lateral diverticulum of the inflated basal section of vesica; and the entire length of the vesica is somewhat shorter (in comparison with the total length of phallus) than in *A. fatidica* and *A. mayrorum*.

In the female genitalia, the apophyses anteriores are longer and the appendix bursae is somewhat shorter than in *A. fatidica*; the ovipositor and the ductus bursae are proportionally shorter, and the appendix bursae is shorter than in *A. mayrorum*.

Description. Wingspan: males 40–41 mm, female 32 mm. The main external features are typical of the *A. fatidica* species-complex. Forewing ground colour pale greyish-brown or slate-grey, with darker grey and brown irroration; costa and veins darker than ground colour and defined broadly with paler ochreous-grey intervenal stripes. Antemedial line variably but strongly marked, partly obsolete; median fascia absent; median area usually less variegated than in the other related species. Postmedial line recognisable though diffuse, pale ochreous-grey, and defined by a row of dark dots; its upper part curved inwards rather strongly around reniform stigma. Subterminal line obsolescent, ochreous-grey, defined by a row of conspicuous intervenal chevron-spots; terminal line fine, black(ish), with weak or indistinct dark dots; cilia ochreous-grey, with variably strong brown midline. Stigmata well-defined, medium-sized or relatively small, outlined by black or dark blackish-brown; claviform stigma long, dark, blackish-brown with only a slightly paler filling; orbicular stigma rather small, usually flattened-elliptical (drop-shaped) with pointed posterior edge and darker brown centre. Reniform stigma medium-sized, elliptical or lunulate, with more or less diffuse dark grey-brown outline and filling (which is stronger than in *A. mayrorum*); intracellular dark patch between stigmata blackish-brown or blackish.

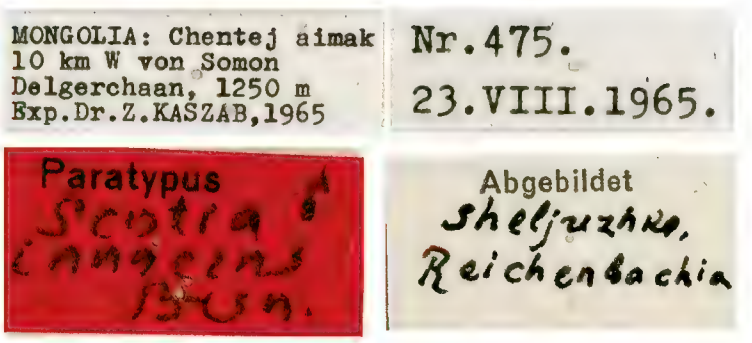
Hindwing milky-white or light whitish-grey with fine ochreous shade, costal area, termen and diffuse marginal stripe with ochreous-brown or greyish suffusion of variable strength; veins darkened. Discal spot rounded or somewhat lunulate, often shadow-like; terminal line more or less continuous, brownish; cilia whitish with some pale brownish shading. Forewing underside rather unicolorous grey, suffused with fuscous, discal dot and postmedial line obsolescent or missing. Hindwing underside whitish with darker veins, reduced transversal line and relatively well-defined discal spot; terminal line fine, brown, without or with only very small darker dots.

Molecular data. BIN URI: BOLD: ACR9899. The intraspecific average and maximum distances of the barcode region are 0% (p-dist) (n=3), however intraspecific divergence may increase with additional samples from the Pyrenees. The minimum distance to the nearest neighbour *Agrotis mayrorum* is 1.12%, whereas the minimum distance to *Agrotis fatidica* is 2.18%.

Bionomics. Host-plant and early stages are unknown. The adults fly relatively late in the season, the specimens of the type series were collected in early August. Most of the specimens were obtained by light trapping using UV tubes and mercury vapour lamp. Adult records are restricted to alpine meadows and scree at high altitudes above the timberline (2200–2300 m a.s.l.).

Distribution. The new species is known from the eastern Pyrenees in France and Spain. The type-series originates from the French side of the Pyrenees; the occurrence of the species on the Spanish side is documented by Redondo et al. (2010, under the name *A. fatidica*).

49. *Agrotis innocens* (Boursin, 1967) Paratype male

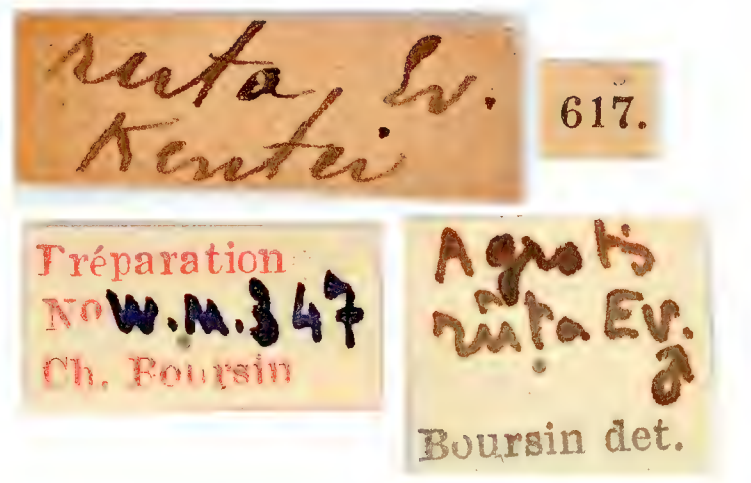


50. *Agrotis innocens* (Boursin, 1967) Paratype male, labels

51. *Agrotis ruta* (Eversmann, 1851) male

52. *Agrotis ruta* (Eversmann, 1851) male, labels

53. *Agrotis ruta* (Eversmann, 1851) male



54. *Agrotis ruta* (Eversmann, 1851) male, labels

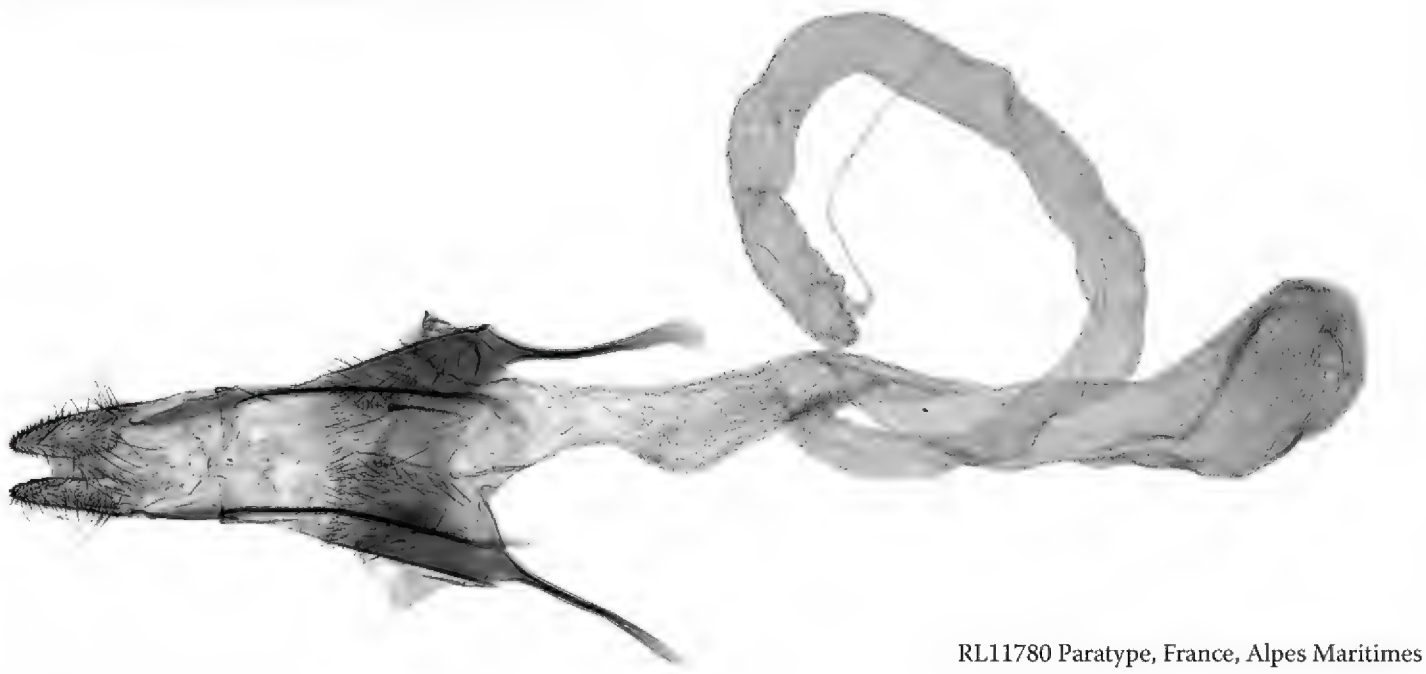
55. *Agrotis ruta* (Eversmann, 1851) male
(Holotype of *Agrotis xylographa* Boursin, 1948)

56. *Agrotis ruta* (Eversmann, 1851) male, labels
(Holotype of *Agrotis xylographa* Boursin, 1948)

Figures 49–56. 49–50 *Agrotis innocens*, paratype male, Mongolia; **51–56** *Agrotis ruta*, **51–52** male, Russia, **53–54** male, Mongolia, **55–56** male, Russia (holotype of *Agrotis xylographa*).

RL11834 Austria, Carinthia

Gen. fig. 16. *Agrotis fatidica* (Hübner, 1824)



RL11780 Paratype, France, Alpes Maritimes

Gen. fig. 17. *Agrotis mayrorum* **sp. n.**

RL11312 Paratype, France, Pyrenees

Gen. fig. 18. *Agrotis mazeli* **sp. n.**

Gen. figs 16–18. 16 *Agrotis fatidica*, female genitalia, Austria, **17** *Agrotis mayrorum* sp. n., paratype, female genitalia, France, **18** *Agrotis mazeli* sp. n., paratype, female genitalia, France.

57. Type-locality of *Agrotis mayrorum* **sp. n.**

58. Type-locality of *Agrotis mayrorum* **sp. n.**

59. Type-locality of *Agrotis mayrorum* **sp. n.**

Figures 57–59. The type-locality of *Agrotis mayrorum*.

Discussion

Taxonomic considerations

The vast majority of European Noctuinae species are well-defined by morphological characters such as phenotypical appearance and genitalia structures. However, remarkable exceptions are found in some genera, e.g. *Diarsia* Hübner, 1821, *Xestia* Hübner, 1818, *Euxoa* Hübner, 1821, and *Agrotis* Ochsenheimer, 1816, all of which include cryptic and/or disputed taxa. The *Agrotis fatidica*-group belongs to such a disputed species-complex reflected by unstable taxonomic treatment in various monographic papers (e.g. Fibiger 1997; Fibiger et al. 2010; Gyulai et al. 2017; Hreblay et al. 1998; Hreblay and Ronkay 1998; Kononenko 2005; Nupponen et al. 2001; Volynkin 2012), and through the description of two new species from Europe during the last few decades, namely *A. proverai* from Italy (Fibiger et al. 2010) and *A. luehri* from Norway (von Mentzer and Moberg 1987). In this paper, we have examined the congruence of these classical and morphologically-driven species concepts using molecular data, which has resulted in a reformulated picture of the taxonomy.

We treat *A. luehri* as a Scandinavian subspecies of *A. fatidica*, a decision that means the species *fatidica* is now perceived to have an arctic-alpine distribution. By contrast, the southwestern alpine and Pyrenean populations previously treated as *A. fatidica* are separated from our revised concept of the species both by morphology and by molecular data of the DNA barcode region. We have described these residual alpine populations of *'A. fatidica'* into two new species — *A. mayrorum* and *A. mazeli*. DNA barcoding resulted in excellent support for delimitation of the two alpine species with a distinct barcode gap of about a minimum of 1.7% and a very low intraspecific divergence. *A. proverai* from the Central Italian Apennines, however, which can be separated from its alpine relatives by morphology, is only weakly separated from typical *A. fatidica* by a barcode gap of about 0.5% and both species share their BIN. We consider even this low but constant distance as interspecific, a hypothesis which is supported by the generally low divergence in the entire species-group. Examples are the morphologically readily separated *A. ruta* and *A. robusta* from North America, with only small distances of roughly 1% to taxa of the *A. fatidica* species-group from Europe.

Of relevance here is that the *A. fatidica* species-group is considered by authors to be most closely related to the *A. segetum* species-group, notably to *A. clavis*, according to their larval morphological features (Nupponen et al. 2001). However, our molecular data (DNA barcodes) do not confirm this statement, and place the *A. fatidica*-group in the Palaearctic fauna nearest to the *A. vestigialis*- and the *A. cinerea*-groups.

Biogeography

All western Palaearctic species treated here show an allopatric pattern of distribution. *Agrotis mayrorum* (SW Alps), *A. mazeli* (Pyrenees) and *A. proverai* (Apennines) occur in well separated mountain systems, while *A. fatidica* in Europe occurs in the Alps and Scandinavia, with closely related or conspecific populations from the Balkans and from Ural to Central Asia which need further investigation. It seems likely that the species was widely distributed in the tundra belt during glacial periods and was able to spread quickly from hypothetical refugia perhaps north of the Alps or from Eastern Europe and Asia to formerly glaciated regions in the North and South after the last cold period. Similar movements are known in other species of Lepidoptera such as *Hepialus humuli* (Linnaeus, 1758) (Hepialidae) (Simonsen and Huemer 2014). The present disjunct distribution pattern is interpreted as a consequence of warmer postglacial periods which induced an increasing isolation of populations.

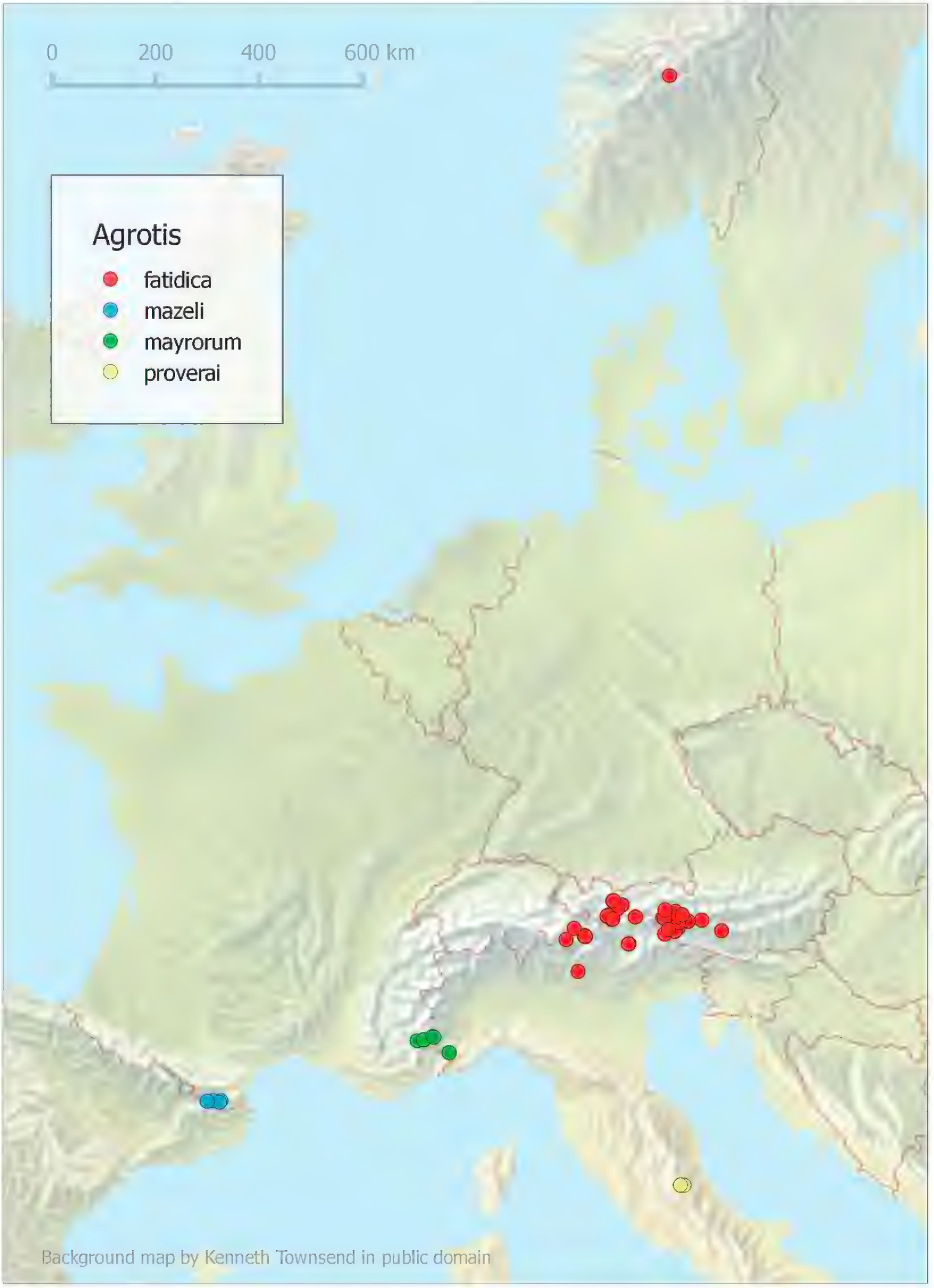


Figure 60. Distribution pattern of successfully sequenced records of the *A. fatidica*-complex in Europe.

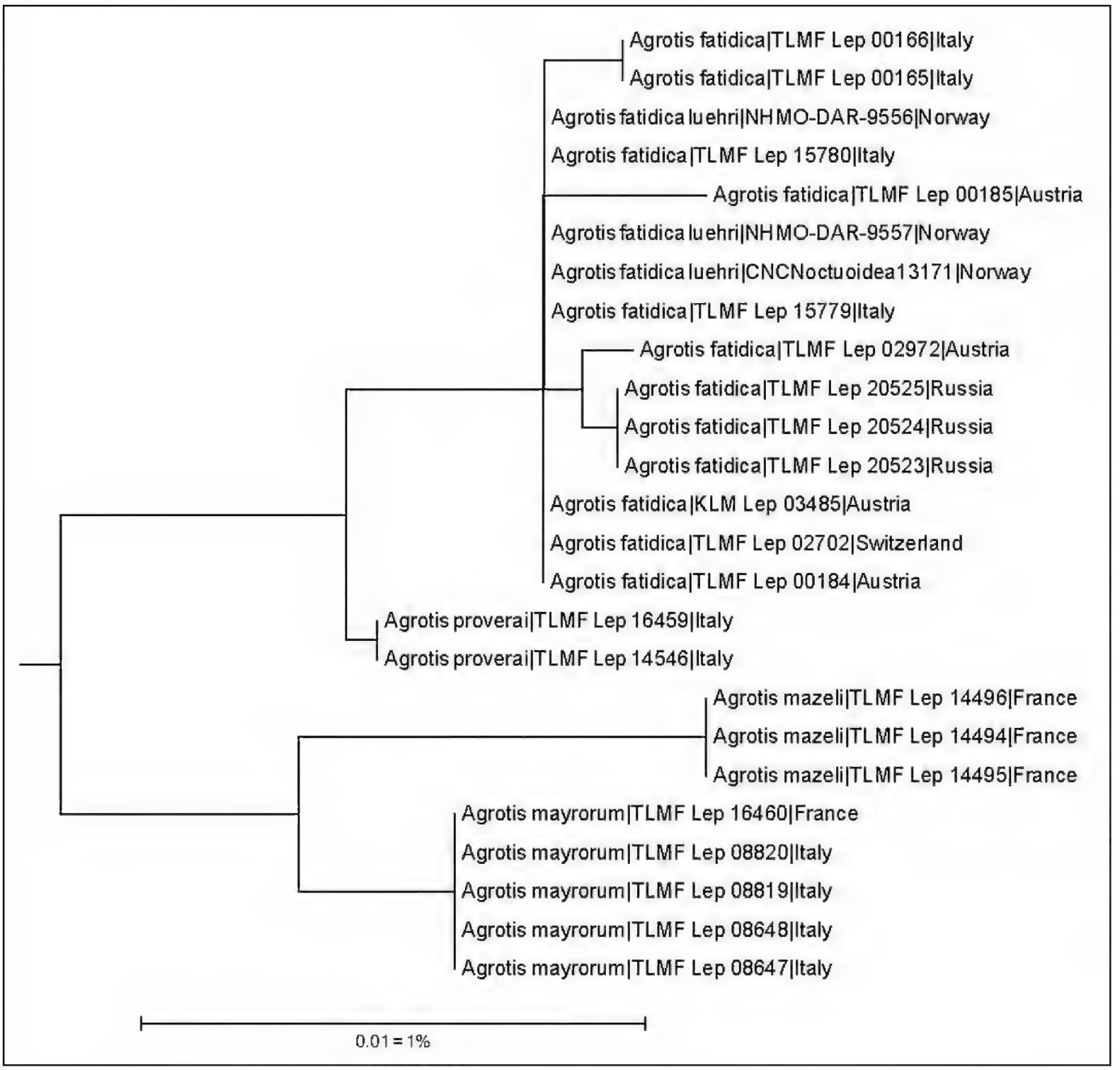


Figure 61. Neighbor Joining tree of the *A. fatidica*-complex in Europe (Kimura 2 parameter, built with MEGA 6; cf. Tamura et al. 2013), only sequences >580 bp considered. Source: DNA barcode data from BOLD (Barcode of Life Database, cf. Ratnasingham & Hebert 2007).

The distribution of *A. fatidica* in the Alps is discontinuous and patchy. It is widely distributed in the central eastern Alps from western Styria (south-eastern Austria) to Graubünden (eastern Switzerland), but almost completely absent from the northern and southern mountain ridges with e.g. only a single population known from the Italian Dolomites. In the western Alps just a few Swiss (Wallis) localities are reported (Wyman et al. 2015) and none southwards (Parenzan and Porcelli 2005–2006), indicating a considerable distribution gap from *A. mayrorum* (see Fig. 60). It seems likely that separation of these two species from a common ancestor may date back several glacial periods (see also Huemer and Hausmann 2009).

Surprisingly the nearest species, in terms of the DNA barcode, to typical *A. fatidica* is not *A. mayrorum* from the SW Alps but *A. proverai* from the Apennines. One might have expected that gene flow

between populations from the SW Alps and the Apennines would be much more likely than from the eastern Alps to central Italy due to almost continuous mountain systems connecting the Apennines with the SW Alps. However, the barcode distance of *A. proverai* and *A. mayrorum* with 1.55% is considerably greater than that between *A. fatidica* and *A. proverai* (ca. 0.5%), thus indicating a much longer isolation of these taxa. A similar pattern of distribution is documented for only few alpine species, e.g. *Aspilapteryx spectabilis* Huemer, 1994 (Gracillariidae), which is only known from the eastern Alps and the Central Italian Apennines but absent from the SW Alps (Huemer 2011). However, in the absence of molecular evidence these widely separated populations of this latter species are considered conspecific.

Acknowledgements

We are particularly grateful to Paul Hebert and his team at the Canadian Centre for DNA Barcoding (Guelph, Canada) whose sequencing work was enabled by funding from the Government of Canada to Genome Canada through the Ontario Genomics Institute. We are also grateful to the Ontario Ministry of Research and Innovation and to NSERC for their support of the BOLD informatics platform.

We are indebted to the Promotion of Educational Policies, University and Research Department of the Autonomous Province of Bolzano - South Tyrol for helping to fund the project "Genetische Artabgrenzung ausgewählter arktoalpiner und boreomontaner Tiere Südtirols", and the Austrian Federal Ministry of Science, Research and Economics for funds received in the framework of ABOL (Austrian Barcode of Life).

Hannes Kühtreiber (TLMF) is acknowledged for his kind assistance with the production of the map (Fig. 60). We thank Robert Mazel (Perpignan, France), Serge Peslier (Perpignan, France), Martin Honey and Alberto Zilli (BMNH), Ole Karsholt (ZMUC, Copenhagen), Martin Lödl and Sabine Gaal (NHM Vienna), Wolfram Mey (MNHU Berlin) Tobias Malm (RNS Stockholm), Bjarne Skule (Veksø), and Christian Wieser (Landesmuseum Kärnten, Klagenfurt) for providing material for our examination, and Leif Aarvik (Natural History Museum, University of Oslo), Paul Hebert (University of Guelph, Canada) and Don Lafontaine (CNC Ottawa) for access to private barcode data on BOLD. We are particularly grateful to Gábor Ronkay for his advices and the photographs of the moths and their genitalia.

We express our gratitude to the referees, Vladimir S. Kononenko (IBP Vladivostok), José Luis Yela (UCLM Toledo) and an anonymous colleague for their careful work and useful suggestions, and to our copy editor for the accurate work.

Finally, we thank Toni and Marlies Mayr (Feldkirch, Austria) for their invaluable assistance during field research and their generous support with material.

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